TRACKING CARBON SOURCES THROUGH AN ARCTIC MARINE FOOD WEB:

INSIGHTS FROM FATTY ACIDS AND THEIR CARBON STABLE ISOTOPES

By

Shiway Wang

RECOMMENDED:

Dr. Suzanne Budge

Dr. Lara Horstmann-Dehn

Dr. Katrin Iken

Dr. Alan Springer

Dr. Matthew Wooller, Advisory Committee Chair

Dr. Brenda Konar
Head, Program, Marine Sciences and Limnology

APPROVED:

Dr. Michael Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger
Dean of the Graduate School

8/15/14
Date

TRACKING CARBON SOURCES THROUGH AN ARCTIC MARINE FOOD WEB: INSIGHTS FROM FATTY ACIDS AND THEIR CARBON STABLE ISOTOPES

A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

Shiway W. Wang, B.S., M.S.

Fairbanks, Alaska

August 2014

ABSTRACT

Marine production across the Bering-Chukchi continental shelf is influenced by seasonal sea ice dynamics and climatic conditions. Of particular importance is variability in the magnitude and timing of annual phytoplankton production in the water column and in sea ice, and effects of such variability on food web composition and productivity. Of primary concern is the long-term effect of the projected loss of Arctic sea ice on ecosystem productivity and stability, and the fate of upper trophic level species. I examined a portion of the Bering-Chukchi Sea food web by analyzing the fatty acid composition and stable carbon isotope ratios of individual fatty acids in particulate organic matter from sea ice and the water column. These techniques were used to make inferences about diets of three species of zooplankton (*Themisto libellula*, *Calanus marshallae/glacialis*, *Thysanoessa raschii*) sampled during a recent climatically cold, relatively heavy sea ice period in the Bering Sea. I also analyzed fatty acids of four species of ice-associated seals—ringed (*Pusa/Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*)—sampled during the same relatively cold period (2007-2010) as well as a preceding warm (2002-2005), relatively low sea ice period in the Bering Sea. Particulate organic matter from sea ice and the water column had different fatty acid characteristics, most likely stemming from differences in algal composition. My results also showed that in the Bering Sea cold period, the amphipod *T. libellula* was predominately carnivorous, and the copepod *C. marshallae/glacialis* and euphausiid *T. raschii* were primarily herbivorous, but displayed some degree of omnivory. Across all years (2002-2010), fatty acid composition of ice seals showed clear evidence of resource partitioning among them, and little niche separation between spotted and ribbon seals, which is consistent with previous studies. The fatty acid composition of primarily pelagic feeding adult ringed seals and predominantly benthic feeding adult bearded seals did not differ between the recent warm (2002-2005) and cold (2007-2010) periods in the Bering Sea, suggesting that their diets and possibly food web structures were not affected by these large multiyear environmental fluctuations. Notably however, the stable carbon isotope ratios of individual fatty acids of bearded seals from the Bering Sea cold period were higher than those from the warm period, which suggests that their prey base in the Bering Sea was receiving more input from particulate organic matter from sea ice than the water column during those years. By using the stable carbon isotope ratios of individual fatty acids of particulate organic matter from sea ice and the water column in a series of stable isotope mixing models, I estimated the proportional contribution of fatty acids from sea ice particulate organic matter in *T. libellula*, *C. marshallae/glacialis*, and *T. raschii* collected in 2009 and 2010 as 36–72%, 27–63%, and 39–71%,

respectively. Using a similar set of mixing models, I estimated that adult bearded seals had the highest level of fatty acids from sea ice particulate organic matter (62–80%), followed by spotted seals (51–62%), and then ringed seals (21–60%) in 2009 and 2010. Although estimates could not be made for ribbon seals due to lack of samples in 2009 and 2010, their stable carbon isotope ratios of individual fatty acids from 2003 were very similar to those of spotted seals suggesting that the proportional contribution of fatty acids from sea ice particulate organic matter to ribbons seals was similar to that of spotted seals. Assuming that seals sourced their sympagic fatty acids from the Bering Sea, these results suggest that sympagic production is currently an important contributor to food webs supporting both benthic and pelagic upper trophic level species in years with heavy ice cover in the Bering Sea. Thus, the question is raised—with the projected continuing loss of seasonal sea ice in the Arctic, will organic matter input from sympagic production also decline, and will it be compensated for by pelagic production to balance both pelagic and benthic carbon and energy budgets?

Table of Contents

Page

Signature Page i

Title Page iii

Abstract v

Table of Contents vii

List of Figures x

List of Tables xii

Preface xiii

GENERAL INTRODUCTION 1

CHAPTER 1: Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production 5

Abstract 5

Introduction 6

Materials and Methods 7

Sample collection 7

FA analysis 8

Compound-specific stable isotope analysis of individual FAs 9

Data analysis 10

Results 12

FA content 12

$\delta^{13}C_{FA}$ values 13

Discussion 14

FA content 14

$\delta^{13}C_{FA}$ values 17

Conclusion 19

Page

Acknowledgements 20

References 21

Appendix 1.1 36

Appendix 1.2 37

CHAPTER 2: Zooplankton diets in the Bering Sea inferred using fatty acid and compound-specific stable isotope analyses reveal the relative importance of pelagic and sympagic carbon sources 39

Abstract 39

Introduction 40

Methods 42

Sample collection 42

Fatty acid analysis 43

Carbon stable isotope analysis of individual fatty acids 44

Data analysis 44

Results 46

Fatty acid profiles 46

Fatty acid biomarkers 47

Carbon stable isotopes of fatty acids 48

Discussion 49

Fatty acid biomarkers 49

Fatty acid profiles 50

Carbon stable isotopes of fatty acids 52

Acknowledgements 57

References 58

Appendix 2.1 76

Appendix 2.2 78

Page

CHAPTER 3: Trophic relationships and carbon sources of ice seals during recent environmental shifts in the Bering Sea....79

Abstract....79

Introduction....80

Methods....81

Sample collection....81

Laboratory analysis....83

Data analysis....84

Results....87

Fatty acid profiles....87

$\delta^{13}C_{FA}$ values of fatty acids....88

Discussion....89

Acknowledgements....99

References....100

Appendix 3.1....128

Appendix 3.2....132

Appendix 3.3....140

GENERAL CONCLUSIONS....147

REFERENCES....151

Appendix....159

List of Figures

Page

Figure 1.1 Sampling stations for i-POM and p-POM collected in the Bering Sea in 2010 28

Figure 1.2 Non-metric multidimensional scaling (MDS) plot of i-POM and p-POM 29

Figure 1.3 Proportions of some FAs (mean ± SE) in i-POM and p-POM 30

Figure 1.4 (a) Diatom FA indicators and dinoflagellate indicator and (b) bacterial FA indicator in i-POM and p-POM 31

Figure 1.5 Boxplot of concentrations of 13 FAs in the water column 32

Figure 1.6 $\delta^{13}C_{FA}$ values for 13 select FAs (mean ± SE) in i-POM and p-POM 33

Figure 1.7 (a) Day length and $\delta^{13}C_{FA}$ values for FA 16:1n-7 in i-POM and p-POM, (b) isotopic fractionation (Δ) in a closed system 34

Figure 1.8 Day length and fraction of source dissolved inorganic carbon reacted for 12 FAs of i-POM during maximum ice extent conditions in 2010 35

Figure 2.1 Sampling stations for *Themisto libellula, Calanus marshallae/glacialis,* and *Thysanoessa raschii* 71

Figure 2.2 nMDS plot of *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii* 72

Figure 2.3 Proportions of select fatty acids in *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii* 73

Figure 2.4 Biplot of the carnivory marker (18:1n-9/18:1n-7) and the diatom marker (16:1/16:0) for *Themisto libellula, Calanus marshallae/glacialis*, and *Thysanoessa raschii* 74

Figure 2.5 $\delta^{13}C$ values for six fatty acids in (a) *Themisto libellula,* (b) *Calanus marshallae/glacialis*, and (c) *Thysanoessa raschii* 75

Figure 3.1 Map showing the locations of Alaska Native subsistence communities where blubber samples of adult ringed, bearded, spotted, and ribbon seals were collected 119

Figure 3.2. nMDS plot of adult ringed and bearded seals using fatty acid (FA) profiles from warm and cold years in the Bering Sea 120

Figure 3.3. Proportions of non-methylene interrupted (NMI) fatty acids (FAs) found in full-thickness blubber of adult ringed and bearded seals during warm and cold years in the Bering Sea 121

Page

Figure 3.4. Biplot of the distance-based redundancy analysis (dbRDA) relating the variability of fatty acid (FA) composition of adult ringed, bearded, spotted, and ribbon seals 122

Figure 3.5. Proportions of fatty acids (FAs) > 1% that were primarily responsible for the significant difference (PERMANOVA $P<0.001$) in full-thickness blubber FA composition among adult ringed, bearded, and spotted seals as indicated by SIMPER analysis 123

Figure 3.6. Proportions of non-methylene interrupted fatty acids (FAs) in full-thickness blubber of adult ringed, bearded, spotted, and ribbon seals 124

Figure 3.7. $\delta^{13}C$ values for 11 fatty acids (FA) of adult bearded seals in 2004 – 2005 (Bering Sea warm period; n=32) and 2007 – 2010 (Bering Sea cold period; n=48) 125

Figure 3.8. Non-metric multidimensional scaling (nMDS) plot of the $d^{13}C_{FA}$ values of 11 fatty acids of adult ringed, bearded, spotted, and ribbon seals 126

Figure 3.9. $\delta^{13}C$ values for 11 fatty acids of adult ringed, bearded, spotted, and ribbon seals. 127

List of Tables

Page

Table 2.1 Sample information for i-POM and p-POM collected from the Bering Sea shelf in 2009 66

Table 2.2 $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 from i-POM and p-POM collected in the Bering Sea in 2009 and 2010 67

Table 2.3 Fatty acid (FA) biomarkers for (a) *Themisto libellula*, (b) *Calanus marshallae/glacialis*, and (c) *Thysanoessa raschii* collected in 2009 and 2010 68

Table 2.4 Percentages for 16:1n-7, 20:5n-3, and 22:6n-3 from i-POM and p-POM in 2009 and 2010 69

Table 2.5 Estimates of i-POM (%) in *Themisto libellula, Calanus marshallae/glacialis*, and *Thysanoessa raschii* from four SIAR mixing models (a) without and (b) with concentration dependencies 70

Table 3.1. Samples sizes for full-thickness blubber collected from adult ringed, bearded, spotted, and ribbon seals by year and season 111

Table 3.2. PERMANOVA analysis results of adult ringed and bearded seal fatty acid profiles between spring-summer and fall-winter months 112

Table 3.3 PERMANOVA analysis results of adult ringed, bearded, and spotted seal fatty acid profiles among years 113

Table 3.4 PERMANOVA analysis results of adult bearded seal fatty acid profiles between Little Diomede and Point Hope in 2005, 2006, 2009, and 2010 114

Table 3.5. *P* values for the results from (a) Mann-Whitney U-test comparing each non-methylene interrupted (NMI) fatty acids (FAs) from Bering Sea warm and cold years for adult ringed and bearded seals and (b) Kruskal-Wallis ANOVA with multiple comparisons of NMI FAs among adult ringed, bearded, spotted, and ribbon seals 115

Table 3.6 PERMANOVA analysis results of bearded and spotted seal $\delta^{13}C_{FA}$ values among years 116

Table 3.7 Percentages for 20:5n-3 and 22:6n-3 from i-POM and p-POM in 2009 and 2010 117

Table 3.8. Estimates of i-POM (%) contribution to adult ringed, bearded, and spotted seals during spring-summer (SS) and fall-winter (FW) in 2009 and 2010 from SIAR stable isotope mixing models 118

Preface

This project would not have been possible without the financial support from the following sources: National Science Foundation (ARC-0920177 and 0732767), the North Pacific Research Board Graduate Research Award, the University of Alaska Center for Global Change Student Research Grant with funds from the Cooperative Institute for Alaska Research, Robert and Kathleen Byrd Award, Dieter Family Marine Science Research Scholarship, the Ken Turner Memorial Fellowship, and the Bering Sea Ecosystem Study Project. In addition, I am indebted to the Native subsistence communities of Little Diomede, Gambell, Hooper Bay, Kivalina, Nome, Point Hope, Savoonga, and Shishmaref for providing samples from their subsistence hunts for Chapter 3.

I thank my major advisor, Dr. Mat Wooller, and my committee members, Dr. Sue Budge, Dr. Lara Horstmann-Dehn, Dr. Katrin Iken, and Dr. Alan Springer for their encouragement, patience, and faith in my success, and their efforts to promote my growth as a scientist and human being. I also thank Dr. Rolf Gradinger, Lori Quakenbush, and Dr. Diane O'Brien for their advisement, time, and expertise in their respective fields of research. I thank Jared Weems and Sean Brennan for assisting with sample collections. I am grateful to Tim Howe, Norma Haubenstock, and Cory Graham for laboratory assistance with stable isotope analyses, and Anne Timmins for fatty acid laboratory assistance. I thank my office mate and partner in crime on this project, Laura Oxtoby, and Anna Bryan for providing help and feedback through the duration of this project.

Finally, I thank my parents, sister, and brother for their unwavering support and encouragement through this journey. Last but definitely not least many thanks to Dave, Leo, Max, and Noah for their unconditional love, support, and constant reminders of what is really important in this life.

GENERAL INTRODUCTION

Marine production dynamics across the Bering-Chukchi continental shelf are influenced to a great extent by seasonal sea ice dynamics driven by climatic conditions (Walsh & McRoy 1986, Stabeno et al. 2010, Brown et al. 2011). Of particular importance is the variability in the magnitude and timing of annual phytoplankton production in the water column and in sea ice (sympagic production), and effects of such variability on food web composition and productivity. Of primary concern is the long-term effect of the projected reduction in Arctic sea ice and its associated sympagic community of phytoplankton and zooplankton, due to global climate change, on ecosystem productivity and stability, and the fate of upper trophic level species. Based on observations in this century, Brown et al. (2011) have predicted that annual water column primary production on the Bering Sea shelf will increase with reduced sea ice. An implied corollary is that annual sympagic primary production will decrease, although production budgets of sea ice phytoplankton are poorly understood. Less is known about production dynamics on the Chukchi Sea shelf, but recent evidence suggests that water column primary production may be much higher than was previously estimated (Arrigo et al. 2012, 2014). In both seas, annual production by water column phytoplankton in any year is likely much higher than production by sea ice phytoplankton. For instance, the proportion of the total primary production originating from sea ice algae in the Bering Sea has been estimated to be between as little as 3% and up to 30% (McRoy & Goering 1976, Gradinger unpublished data). This is not to say that sympagic production is unimportant, however, because the timing of primary production events, including sympagic primary production, relative to the needs of grazers, is known to be crucial to their success, and thus to the transfer of carbon and energy to higher trophic levels (Conover & Huntley 1991, Tourangeau & Runge 1991, Michel et al. 1996, Søreide et al. 2008, 2010, Durbin & Casas 2014).

To understand how changes in primary production dynamics due to loss of Arctic sea ice might affect upper trophic level consumers, we need to first understand their diets, and quantify the amount of sympagic carbon that is being transferred to them. The overall goal of my research was to further elucidate Bering-Chukchi Sea pelagic and benthic food web relationships, especially in regard to the relative importance of pelagic and sympagic carbons sources. To do this, I used elemental (carbon stable isotopes) and molecular (fatty acids) biomarkers to characterize pelagic and sympagic organic matter, and to infer dietary relationships among key species of zooplankton and marine mammals, and the degree to which sympagic and pelagic primary production support them.

Fatty acid (FA) analysis has been used to qualitatively study the foraging patterns and diets of Arctic zooplankton (e.g., Sargent & Falk-Petersen 1981, 1988, Falk-Petersen et al. 1990, 2000, Auel et al. 2002, Graeve et al. 2005, Søreide et al. 2013) and marine mammals (e.g., Thiemann et al. 2007a, 2008, Cooper et al. 2009). Unlike traditional methods, such as stomach content analysis, which only provides information on the most recent meal, FA analysis can give qualitative insight on the longer-term diet of animals (e.g., Iverson et al. 1997). In addition to using a suite of FAs (termed FA profiles or signatures) to infer dietary patterns, specific FA biomarkers have been used in many applications. For instance, FAs have helped determine the sources of primary production (diatoms versus dinoflagellates) to zooplankton in Arctic Seas (Scott et al. 1999, Falk-Petersen et al. 2000, Scott et al. 2001, Hop et al. 2006, Søreide et al. 2008, Falk-Petersen et al. 2009, Søreide et al. 2013), infer levels of omnivory and carnivory in zooplankton (Falk-Petersen et al. 1990, Graeve et al. 1997, Falk-Petersen et al. 2000, Auel et al. 2002, Kürten et al. 2013), and also determine the presence of benthic prey in marine mammals (Budge et al. 2007, Thiemann et al. 2007b, Cooper et al. 2009). FA biomarkers have also been used to detect the presence of sea ice algae in zooplankton diets (Scott et al. 1999, 2001). Because the same FAs (e.g., 16:4n-1 and 20:5n-3) can characterize diatoms from both sea ice and the water column, using FA biomarkers alone to differentiate sympagic and pelagic organic matter in marine food webs is insufficient (i.e., Søreide et al. 2008). However, the carbon stable isotope values of specific FAs (expressed as $\delta^{13}C_{FA}$) have been found to be relatively higher in sea ice algae than in pelagic phytoplankton (Budge et al. 2008). These isotopic differences have been used to estimate the proportional contribution of sympagic and pelagic primary production to consumers in the Arctic (Budge et al. 2008).

In this dissertation, I described the FA and carbon stable isotope characteristics of particulate organic matter from sea ice (i-POM, a proxy for sympagic phytoplankton) and the water column (p-POM, a proxy for water column phytoplankton) during a recent climatically cold, relative heavy sea ice period in the Bering Sea, and then used these techniques to make inferences about diets of three species of zooplankton (the amphipod *Themisto libellula*, the copepod *Calanus glacialis/marshallae*, and the krill *Thysanoessa raschii*). These zooplankters are key trophic links in the transfer of carbon and energy from primary producers to higher trophic levels in the Bering Sea, because they are important prey for marine fishes, seabirds, and mammals (Frost & Lowry 1981, Springer & Roseneau 1985, Baier & Napp 2003, Ciannelli et al. 2004, Pinchuk et al. 2013, Strasburger et al. 2013). Although important as prey, the diets of these zooplankton species in the Bering Sea are not well known, but are thought to be similar to those in other high latitude seas (e.g., Pinchuk et al. 2013). *T. libellula* is a predatory amphipod (Marion et

al. 2008, Noyon et al. 2009), while *Calanus marshallae* and *C. glacialis* are predominately herbivores, but can be omnivorous (Smith 1990, Hobson et al. 2002, Sato et al. 2002, Baier & Napp 2003, Stevens et al. 2004), and *T. raschii* is also considered mainly an herbivore, but can also be carnivorous and may switch to detrital feeding during the winter (Mauchline & Fischer 1969, Falk-Petersen et al. 1981, Sargent & Falk-Petersen 1981, Smith 1991, Hagen & Auel 2001, Hop et al. 2006). All of these zooplankton species are known to have some degree of association with sea ice algae in seasonally ice-covered seas (e.g., Conover & Huntley 1991, Tourangeau & Runge 1991, Michel et al. 1996, Auel et al. 2002, Baier & Napp 2003, Søreide et al. 2006, Budge et al. 2008, Søreide et al. 2008, 2013, Durbin & Casas 2014).

I also used FA and compound-specific carbon stable isotope techniques to make inferences about diets and primary carbon sources of four species of ice-associated pinnipeds – ringed (*Pusa*/*Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*) – in the cold period (2007-2010) and a preceding warm (2002-2005), relatively low sea ice period in the Bering Sea. These seals are collectively known as 'ice seals' because of their high degree of association with sea ice. They depend on ice to provide an important platform for hauling-out, pupping, molting, and as a base for foraging trips (Fay 1974), and thus, they are supported by prey in seasonally ice covered waters. In part because of potential changes in diet due to sea ice loss from climate change, and consequences to individual and population health, the Arctic Basin population of ringed seals and the Pacific population of bearded seals were listed as threatened under the provisions of the U. S. Endangered Species Act in 2012 (NMFS 2012a, b). The feeding ecology and habitat preferences of ice seals differ between species within the sea ice environment (e.g., Simpkins et al. 2003). Ringed seals are found in heavy ice including coastal land-fast ice, and primarily consume Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), and crustaceans (e.g., gammarid amhipods, euphausiids, and shrimps) (McLaren 1958, Lowry et al. 1980a, Dehn et al. 2007, Quakenbush et al. 2011). In contrast, bearded seals predominately feed on benthic organisms, typically avoid heavy ice cover, and are found in drifting pack ice in relatively shallow shelf waters (Lowry et al. 1980b, Burns et al. 1981, Simpkins et al. 2003, Dehn et al. 2007). However, they also feed on pelagic prey, possibly when benthic prey are not available (e.g., Finley & Evans 1983, Antonelis et al. 1994, Dehn et al. 2007, Carroll et al. 2013). Spotted seals tend to stay near the southern ice edge and avoid regions of thicker ice in winter and spring, but they spend the summer in coastal waters often hauling-out on land (Fay 1974, Burns 2002). They feed primarily on fishes, but also crustaceans and cephalopods (e.g., Bukhtiyarov et al. 1984, Dehn et al. 2007, Quakenbush et al.

2009). Similarly, ribbon seals are found in the southern seasonal pack ice during the breeding season (Burns 1971, Fay 1974, Lowry 1985, Kelly 1988) and consume a range of pelagic and benthic prey, such as shrimps, crabs, mysids, cephalopods, and fishes including walleye pollock (*Theragra chalcogramma*), eelpout (*Lycodes* spp.), capelin (*Mallotus villosus*), Arctic cod, and saffron cod (e.g., Burns 1971, Frost & Lowry 1980, Dehn et al. 2007, Ziel et al. 2008). Although none of these seals are direct consumers of primary productivity, they are linked to sympagic and pelagic primary production through their prey.

Chapter 1 describes and compares the FA and $\delta^{13}C_{FA}$ values of sea ice and pelagic organic matter (i-POM and p-POM, respectively) in the Bering Sea. Chapter 2 examines and compares the foraging strategies of zooplankton (*T. libellula, C. marshallae/glacialis, and T. raschii*), and uses the information from Chapter 1 to estimate the proportional contribution of FAs from sympagic relative to pelagic organic matter to zooplankton. Similarly, Chapter 3 compares and contrasts resource partitioning of bearded, ringed, spotted, and ribbon seals, and uses the information from Chapter 1 to estimate the proportional contribution of FAs from sympagic relative to pelagic organic matter to ice seal species. In my final conclusions, I summarize my findings, place them in the broader context of food web dynamics, speculate on how future changes in loss of sea ice might affect my study species, and make recommendations for future research.

CHAPTER 1:

Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production[1]

Abstract

We determined fatty acid (FA) profiles and carbon stable isotopic composition of individual FAs ($\delta^{13}C_{FA}$ values) from sea ice particulate organic matter (i-POM) and pelagic POM (p-POM) in the Bering Sea during maximum ice extent, ice melt, and ice-free conditions in 2010. Based on FA biomarkers, differences in relative composition of diatoms, dinoflagellates, and bacteria were inferred for i-POM versus p-POM and for seasonal succession stages in p-POM. Proportions of diatom markers were higher in i-POM (16:4n-1, 6.6–8.7 %; 20:5n-3, 19.6–25.9 %) than in p-POM (16:4n-1, 1.2–4.0 %; 20:5n-3, 5.5–14.0 %). The dinoflagellate marker 22:6n-3/20:5n-3 was highest in p-POM. Bacterial FA concentration was higher in the bottom 1 cm of sea ice (14–245 μg L^{-1}) than in the water column (0.6–1.7 μg L^{-1}). Many i-POM $\delta^{13}C_{FA}$ values were higher (up to~10 ‰) than those of p-POM, and i-POM $\delta^{13}C_{FA}$ values increased with day length. The higher i-POM $\delta^{13}C_{FA}$ values are most likely related to the reduced dissolved inorganic carbon (DIC) availability within the semi-closed sea ice brine channel system. Based on a modified Rayleigh equation, the fraction of sea ice DIC fixed in i-POM ranged from 12 to 73 %, implying that carbon was not limiting for primary productivity in the sympagic habitat. These differences in FA composition and $\delta^{13}C_{FA}$ values between i-POM and p-POM will aid efforts to track the proportional contribution of sea ice algal carbon to higher trophic levels in the Bering Sea and likely other Arctic seas.

[1] Published as Wang SW, Budge SM, Gradinger RR, Iken K, Wooller MJ (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699-712

Introduction

The contribution of ice algae to total primary production in the seasonally ice-covered Bering Sea is estimated to be between 3 and 30 % (McRoy and Goering 1976; R. R. Gradinger, unpublished data). Thus, the quantitative importance of sea ice algae to marine food webs in Arctic seas such as the Bering Sea remains uncertain (Hobson et al. 1995; Søreide et al. 2006; Budge et al. 2008). In the Bering Sea, the timing of sea ice melt determines the timing of spring phytoplankton blooms, the sources of spring primary production (sympagic or pelagic), and the fate of carbon from this primary production to the marine food web (Walsh and McRoy 1986; Hunt et al. 2002, 2011; Hunt and Stabeno 2002). Climate-related changes in the timing of seasonal sea ice cover affect spring primary production patterns (Stabeno et al. 2001, 2010; Hunt and Stabeno 2002), and these changes will likely propagate through the food web to upper trophic levels (Grebmeier et al. 2006; Bluhm and Gradinger 2008; Leu et al. 2011; Grebmeier 2012). Furthermore, climate-induced changes in the food quality, such as fatty acid (FA) content derived from sympagic and pelagic primary production, could ultimately influence upper trophic levels (Litzow et al. 2006; Leu et al. 2011).

FA profiles and biomarkers of sea ice algae and phytoplankton have been used to understand the feeding ecology of consumers in a wide range of Arctic seas (e.g., Lewis 1969; Falk-Petersen et al. 1998; Auel et al. 2002; Peters et al. 2004; Budge et al. 2007; Mayzaud et al. 2013). Changes in phytoplankton species composition, productivity, physiological state, and amount of living versus decayed material within the marine particulate organic matter (POM) pool can be inferred from variations in FA profiles of POM (Mayzaud et al. 1989; Reuss and Poulsen 2002; Mayzaud et al. 2013). In addition to FA biomarkers, bulk carbon stable isotopic analyses of organisms have been used to examine the feeding ecology of Arctic marine organisms and food webs (e.g., Dehn et al. 2007; Iken et al. 2010; Feder et al. 2011; Weems et al. 2012). In response to increased seasonal light availability (Gradinger et al. 2009) and a carbon-limiting environment of the closed sea ice system (e.g., Fischer 1991; Schubert and Calvert 2001; Kennedy et al. 2002), POM in sea ice (i-POM) has carbon stable isotope values (expressed here as $\delta^{13}C$ values) that are more enriched in ^{13}C than pelagic POM (p-POM) (Hobson et al. 1995; Naidu et al. 2000; Schubert and Calvert 2001; Gradinger et al. 2009; Thomas et al. 2010). In a combination of FA and stable isotope analysis methods, carbon stable isotope analysis of specific FAs ($\delta^{13}C_{FA}$ values, e.g., 16:4n-1 and 20:5n-3) in sea ice algae and pelagic phytoplankton have been investigated (Budge et al. 2008). Sea ice algae $\delta^{13}C_{FA}$ values were higher than

pelagic phytoplankton, which allowed for the quantitative estimation of the proportional contribution of sympagic and pelagic primary production to consumers in the Arctic (Budge et al. 2008).

The $\delta^{13}C_{FA}$ data from sea ice algae and marine phytoplankton so far have been restricted to the Chukchi Sea region off of Barrow, Alaska (Budge et al. 2008). Furthermore, the temporal and spatial variability of $\delta^{13}C_{FA}$ values from marine algae from high latitudes, and the processes that generate this isotopic variability, are poorly resolved. Elucidating these patterns and processes in the Bering Sea is important to help interpret $\delta^{13}C_{FA}$ values at higher trophic levels as a way of estimating the importance of sea ice algal carbon and pelagic carbon to food web production. Our goals were to characterize the FA profiles and the $\delta^{13}C_{FA}$ values of i-POM and p-POM in the Bering Sea, examine seasonal differences, and determine if there was a correlation between $\delta^{13}C_{FA}$ values and day length (used here as a proxy for light availability).

We hypothesize that differences in FA profiles between POM types can be explained by variation in algal taxon composition. In addition, greater seasonal availability of light at the most southerly sea ice locations in the Bering Sea should stimulate the highest levels of sea ice primary production (McRoy and Goering 1974). This high primary production within the sea ice habitat would then lead to a subsequent ^{13}C enrichment of individual FAs as a result of decreased isotopic discrimination during photosynthesis in the carbon-limited and closed sympagic habitats.

Materials and methods

Sample collection

i-POM and p-POM samples were collected as part of the Bering Sea Ecosystem Study/Bering Sea Integrated Ecosystem Research Program during three major seasonal ice regimes in 2010 based on timing of sea ice conditions in the northern and central portions of the Bering Sea: maximum ice extent (13-28 March; i-POM n = 12, p-POM n = 14), ice melt (11 May-10 June; i-POM n = 1, p-POM n = 20), and ice-free conditions (18 June–10 July; p-POM n = 15) (Fig. 1.1). One p-POM sample was taken from a station in the deep basin of the Bering Sea which did not experience ice cover (Fig. 1.1). Maximum ice extent occurred on 31 March 2010 and all stations on the Bering Sea shelf experienced ice cover between 21 March and 10 April 2010 (Cavalieri et al. 1996; Richter-Menge and Overland 2010). For the determination of i-POM in March 2010, sea ice cores were collected with an ice corer (9 cm inner diameter) and cut into sections of 1–10 cm thickness (Cooper et al. 2013). Data in this study came from

samples taken from the bottom 1-cm sections of the sea ice cores, which were completely melted in the dark and filtered on pre-combusted GF/F filters (melted water volumes ranged from 1.8 to 18.5 mL). The i-POM sample taken during ice melt consisted mainly of Melosira arctica (K. Iken, personal observation) collected from overturned ice floes. During maximum ice extent p-POM samples were collected at 15 m below the surface. During ice melt and ice-free conditions, samples were collected at the chlorophyll maximum layer between a depth of 5–29 m from the surface. Each p-POM sample was collected from a single Niskin bottle and sample volumes were between 200 and 1,500 mL. The algal composition in p-POM samples taken during ice melt was described for some stations and contained *Thalassiosira* sp., *Nitzschia frigida*, *Fragilariopsis* sp., *Chaetoceros* sp., *Pseudonitzschia* sp., and *Phaeocystis* sp. (K. Iken, personal observation). Samples were filtered using a GF/F filter (pore size 0.7 μm) and stored in a vial of chloroform at −20 °C until laboratory analysis.

Details for the determination of ice bulk properties are described by Cooper et al. (2013). In short, filters were dried, acid fumed, and analyzed at the Alaska Stable Isotope Facility (ASIF) at the University of Alaska Fairbanks (UAF) for determination of bulk i-POM particulate organic carbon (POC) concentrations and $\delta^{13}C$ values (Cooper et al. 2013). A second set of filters was analyzed for chlorophyll a concentrations using fluorometric determination after extraction in 90 % acetone.

FA analysis

Lipids were quantitatively extracted from all samples using 2:1 chloroform/methanol at 20–30 parts solvent to sample (Folch et al. 1957; Parrish 1999). FA methyl esters (FAMEs) were prepared using an acidic transesterification (Budge et al. 2006). FAMEs were quantified using temperature- programmed gas chromatography (GC) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30-m-long × 0.25-mm-internal diameter column coated with 50 % cyanopropyl-methylpolysiloxane (DB-23) and linked to a computerized integration system (Varian Star software). Shorthand nomenclature of A:Bn-X was used to describe each FAME, where A represents the number of carbon atoms, B the number of double bonds and X the position of the double bond closest to the terminal methyl group. Approximately 70 FAMEs were identified by comparison of retention times with known standards (Nu Check Prep, Elysian, MN), or using GC-mass spectrometry. Concentrations of each FA were determined from a standard (α-cholestane; Sigma-Aldrich) with a known mass and volume of the sample filtered.

Compound-specific stable isotope analysis of individual FAs

$\delta^{13}C$ of samples (expressed in per mil—‰) were analyzed from FAME sub-samples by routing the effluent from a GC (Trace GC Ultra; Thermo, Bremen, Germany) through a combustion interface (Finnigan GC combustion III; Thermo) to an isotope ratio mass spectrometer (IRMS) (Thermo Finnigan Delta V; Thermo) at ASIF, UAF. The same GC column and method described above for FID analyses of FAMEs were used to separate the FAMEs for analysis using IRMS. To correct for any influence of carbon from the methyl group added during transesterification and determine any kinetic isotope effects, free FA (FFA) standards 16:0 and 18:0 were transesterified with the same reagents described above. The purity of the FFA was confirmed with thin layer chromatography prior to transesterification and $\delta^{13}C$ values for FFA were determined using an elemental analyzer (Costech ECS4010) routed to an IRMS. The $\delta^{13}C$ values of the respective FAMEs of these FFA that had been transesterified into their respective FAMEs were then also measured using the GC-IRMS system described above. We could not perform this analysis on all the FA examined because most are not commercially available. There was no evidence of a kinetic isotope effect associated with transesterification, which is expected for a reaction that goes to completion (Rieley 1994). The difference between the $\delta^{13}C$ values for FFA ($\delta^{13}C_{FFA}$) and FAME ($\delta^{13}C_{FAME}$) with the same chain length was entirely due to the added methyl group. The proportional contribution of this methyl group to a given FA depends on the chain length. Therefore, an average $\delta^{13}C$ value for this added methyl group was calculated using the following equation (Eq. 1.1):

$$(1.1) \qquad \delta^{13}C = (n + 1)[\delta^{13}C_{FAME}] - n[\delta^{13}C_{FFA}],$$

where n is the number of carbon atoms in the FFA (Abrajano et al. 1994). We then calculated an average $\delta^{13}C$ value (-48.8 ± 1.3 ‰, mean ± 1 SD) for the methyl-derived carbon based on the difference between the $\delta^{13}C$ values of the corresponding FFA and their respective FAME. This value was based on three runs each of the C16 and C18 standards, and used to correct our FAME data by applying the above equation. The $\delta^{13}C$ values from the FAMEs were also calibrated using a standard mixture consisting of ethyl and methyl esters of 14:0, 16:0, 18:0, and 20:0 (supplied by Indiana University Stable Isotope Reference Materials) where the coefficient of determination (r^2) of the measured versus expected relationship was >0.99. A C16 laboratory standard was analyzed after every ten samples to track analytical error of the GC-IRMS system, which was ≤ 0.8 ‰ (representing the 1 SD of 14 analyses

of the C16 standard interspersed during the samples runs). All $\delta^{13}C$ values are reported relative to Vienna Pee Dee Belemnite using standard notation, where $\delta^{13}C$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1{,}000$, and R is the corresponding ratio of $^{13}C/^{12}C$.

Data analysis

Bray–Curtis similarity matrices and permutational multivariate ANOVA (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) were used to investigate the variation in FA composition, based on 59 FAs present in proportions >0.1 %, between i-POM and p-POM, and seasonal variation within p-POM using PRIMER version 6 (Primer-E). Non-metric multidimensional scaling plots were used to visualize differences among FA profiles of samples. A stress value of <0.1 indicates good fit of the data with little prospect of incorrect interpretation (Clarke 1993). Similarity percentages routines (SIMPER) were performed to determine FAs contributing most to the observed differences. Data were standardized to 100 % and log(1 + x) transformed prior to analysis.

We examined the proportion of 16:4n-1 and the ratios of 16:1/16:0 and 22:6n-3/20:5n-3 to assess the presence and dominance of diatoms and dinoflagellates in the POM samples (Claustre et al. 1988/1989; Budge and Parrish 1998). Additionally, the sum of 15:0, 17:0, and the iso- and anteiso-FAs (i-14:0, i-15:0, ai-15:0, i-16:0, i-17:0, and ai- 17:0) were used to determine the contribution of bacterial FAs in the POM samples (Budge and Parrish 1998).

$\delta^{13}C_{FA}$ values were determined for 39 FAs. Not all FAs were present in sufficient quantities to be analyzed by GC-IRMS. Out of these 39 FAs, 13 (14:0, 16:0, 16:1n-11/9, 16:1n-7, 16:2n-4, 16:3n-4, 16:4n-1, 18:0, 18:1n-9, 18:2n-6, 18:4n-3, 20:5n-3, and 22:6n-3) were selected for further data analysis because they were identified in most of the samples (63–100 %). FAs 16:1n-11 and 16:1n-9 co-eluted on the GC-IRMS and are referred to here as 16:1n-11/9. Data were not normally distributed, therefore a non-parametric Mann–Whitney U-test was used to assess differences in $\delta^{13}C_{FA}$ values of the selected 13 FAs between i-POM and p-POM during maximum ice extent. A Kruskal–Wallis ANOVA was used followed by Bonferroni adjustment for multiple comparisons to test for differences in $\delta^{13}C_{FA}$ values of each FA in p-POM during maximum ice extent, ice melt, and ice-free conditions. Spearman's rank order correlations were performed to examine any correlations between $\delta^{13}C_{FA}$ values of the 13 selected FAs in both i-POM and p-POM samples and day length. A site-specific estimate of light exposure for each station was determined using the U.S. Naval Observatory website

http://aa.usno.navy.mil/data/docs/RS_OneDay.php. Significance level α was controlled for multiple comparisons with Holm's sequential Bonferroni adjustments. Spearman's rank order correlations were also performed between day length and POM FA concentrations to determine if FA production increased with light exposure (day length). In addition, correlations were examined between day length, POC concentrations, chlorophyll a concentrations, and bulk $\delta^{13}C$ values measured in i-POM to determine if productivity increased with day length within the closed sea ice system.

We estimated the fraction of source ocean water dissolved inorganic carbon (DIC) used for FA synthesis in sea ice during maximum ice extent using the following Rayleigh equation (Eq. 1.2) modified for isotope reaction progress in a closed system (Fry 2006):

$$(1.2) \qquad \delta_{AP} = \delta_{Source} + \Delta * ((1 - f) / f * \ln (1 - f),$$

where, for each FA, the $\delta^{13}C$ value of the accumulated product (δ_{AP}) is the $\delta^{13}C_{FA}$ value measured from i-POM, δ_{Source} is the $\delta^{13}C$ value of ocean water DIC, Δ is the difference between the $\delta^{13}C$ value of the δ_{Source} and instantaneous product (the $\delta^{13}C$ value of product at any instant in time), and f is the fraction or percentage of source (i.e., DIC) reacted. We used two $\delta^{13}C$ values for DIC from previous studies: the mean for surface water of the Pacific Ocean (1.55 ‰) determined by Quay et al. (2003), and the value at the most northerly station in the Pacific Ocean (1.85 ‰) reported by Gruber et al. (1999). p-POM was measured in an open system during the same time and did not vary with day length (see "Results"). Thus, we assumed that the average $\delta^{13}C_{FA}$ value from p-POM during maximum ice extent for each 13 FA could be used to approximate the i-POM $\delta^{13}C_{FA}$ value when the fraction of the source reacted was zero (i.e., p-POM represents i-POM before isotopic discrimination results from the closed sea ice conditions). These values were used to calculate Δ for each FA (Δ = average $\delta^{13}C_{FA}$ of p-POM − δ_{Source}). The fraction reacted for each FA at a given day length was determined using the Solver Function in Microsoft Excel (version 14.3.2 for Mac 2011). Linear regression was performed between day length and the fraction reacted for the 13 selected FAs to determine if day length could be used to predict the fraction of source reacted. The Mann–Whitney U-test, Kruskal–Wallis ANOVA, Spearman's rank order correlations and linear regression were performed using Statistica version 12 (StatSoft).

Results

FA content

The FA profile from the sample from the deep basin was different than that of other samples collected over the Bering Sea shelf during ice melt (Fig. 1.2), and because the station from the deep basin did not experience ice cover it was not included in further data analyses. FA profiles were significantly different between i-POM and p-POM, and also varied seasonally within p-POM (Fig. 1.2; PERMANOVA, $P = 0.001$). Average dissimilarity between i-POM and p-POM FA profiles during maximum ice extent was 31.8 % (SIMPER) with the diatom FAs 16:4n-1 and 20:5n-3 contributing most to the dissimilarity (7.1 and 5.9 %, respectively). These two FAs were present in greater proportions in i-POM (16:4n-1, 6.6–8.7 %; 20:5n-3, 19.6–25.9 %) than in p-POM (16:4n-1, 1.2–4.0 %; 20:5n-3, 5.5–14.0 %). i-POM samples collected during maximum ice extent had lower proportions of 14:0, 16:0, 16:1n-7 and 20:5n-3, and higher proportions of 18:0, 16:1n-11, 18:1n-9, 18:1n-7, 20:1n-7, 16:4n-1, 18:4n-3 and 22:6n-3 compared to the *M. arctica* sample collected during ice melt (Fig. 1.3). Within p-POM, FA profiles were most dissimilar between maximum ice and ice melt conditions (33.7 %, SIMPER). Dissimilarity during maximum ice and ice-free conditions, and ice melt and ice-free conditions was 27.1 and 23.0 %, respectively. FA profiles of p-POM also showed some seasonal patterns with proportions of 16:1n-9, 18:0, 18:1n-9, 20:1n-7 and 22:1n-9 being relatively higher during maximum ice extent, lower during ice melt, and higher again during ice-free conditions. Proportions of 22:6n-3 in p-POM increased seasonally (Fig. 1.3). Total amounts of saturated FA (SAT), monounsaturated FA (MUFA), and polyunsaturated FA (PUFA) varied by POM type and seasonally within p-POM (Fig. 1.3). The amount of SAT from i-POM (22.0–26.3 %) was lower than that from p-POM (26.8–34.9 %). During maximum ice extent and ice melt conditions, levels of MUFA from i-POM were also lower (31.3–32.0 %) than from p-POM (40.6–42.3 %). In contrast, the amount of PUFA from i-POM (41.9–43.8 %) was higher than that from p-POM (18.6–34.8 %).

Diatom biomarkers (16:1/16:0, 16:4n-1) were higher than the dinoflagellate biomarker (22:6n-3/20:5n-3) in i-POM (Fig. 1.4a). This was also observed in p-POM samples during ice melt. However, in p-POM the levels of 16:4n-1 were lower than in i-POM and the ratios of 16:1/16:0 and 22:6n-3/20:5n-3 were similar in p-POM samples during maximum ice extent and ice-free conditions (Fig. 1.4a). The bacterial indicator (i.e., the sum of 15:0, 17:0, and the iso- and anteiso FA) was <4 % of the total FAs in all POM samples (Fig. 1.4b). However, the concentration of the bacterial indicator in the bottom 1 cm of sea ice ranged from 14 to 245 μg L^{-1}, which was on average 115

times greater than the bacterial indicator in the water column during maximum ice extent. The concentrations of the bacterial indicator in the water column during maximum ice extent, ice melt, and ice-free conditions were 0.6 ± 0.3, 1.7 ± 0.8, 0.6 ± 0.2 μg L^{-1} (mean ± SD), respectively.

In March 2010, total concentrations of FAs in the bottom 1 cm of sea ice ranged from 721 to 28,000 μg L^{-1}, which was 60 to almost 1,000 times greater than concentrations measured in the water column (8–542 μg L^{-1}). FA concentrations in the water column showed seasonal change with the highest concentrations measured during ice melt in all FA except for 18:1n-9 (Fig. 1.5). Concentrations of n-3 and n-6 PUFA in the bottom 1 cm of sea ice ranged from 123 to 9,500 and 42–732 μg L^{-1}, respectively. These values were also higher than those found in the water column (n-3 PUFA, 2.9–29.6 μg L^{-1}; n-6 PUFA, 0.8–2.3 μg L^{-1}). FA concentrations in the bottom 1 cm of sea ice increased with day length for all FAs ($R^2 > 0.48$), except 18:1n-9 ($R^2 = 0.16$, Spearman's $P = 0.60$). FA concentrations also increased with increasing POC and chlorophyll a concentrations measured in the bottom 1 cm of sea ice ($R^2 > 0.48$).

$\delta^{13}C_{FA}$ values

The $\delta^{13}C_{FA}$ values of 13 selected FA varied between POM types and among seasonal p-POM samples (Fig. 1.6). During maximum ice extent, $\delta^{13}C_{FA}$ values from i-POM were higher compared with those from p-POM (Mann–Whitney U-test, $P < 0.05$; difference between means ranging from 1.2 to 7.9 ‰), with the exception of 16:2n-4, 16:3n-4, 16:4n-1, and 18:1n-9. Within p-POM samples, $\delta^{13}C_{FA}$ values were significantly different among ice regimes for 18:0 and the unsaturated FAs 16:3n-4, 18:1n-9, 18:2n-6, and 18:4n-3 (Kruskal–Wallis ANOVA, $P < 0.04$; Fig. 1.6). The $\delta^{13}C_{FA}$ values from i-POM increased with increasing day length for all FAs measured (Fig. 1.7a). Correlations between $\delta^{13}C_{FA}$ values of i-POM and day length were significant ($R^2 > 0.73$, Spearman's $P < 0.01$) for all FAs except for 18:1n-9 ($R^2 = 0.50$, Spearman's $P = 0.60$). We found no correlation between $\delta^{13}C_{FA}$ values of the 13 selected FAs in p-POM and day length during maximum ice extent and ice melt conditions (Spearman's $P > 0.05$). Only the $\delta^{13}C_{FA}$ value of 22:6n-3 ($R^2 = -0.73$, Spearman's $P = 0.003$) in p-POM decreased significantly with day length during ice-free conditions.

POC concentration and bulk $\delta^{13}C$ values measured in i-POM during maximum ice extent significantly increased with day length (Spearman's $R^2 > 0.66$, $P < 0.03$). In p-POM, only the concentration of 22:6n-3 significantly increased with day length (Spearman's $R^2 = 0.45$, $P = 0.002$). The average fractionation (Δ) between

ocean water DIC and i-POM during maximum ice extent for the 13 selected FAs ranged from 26.6 to 33.9 ‰ and the percentage of DIC assimilated into FA synthesis at the longest day ranged from 12 to 73 % (Fig. 1.8). Day length and fraction reacted were significantly positively correlated for all FAs ($P < 0.02$), except for 18:1n-9 (Spearman's $R^2 = 0.41$, Fig. 1.8).

Discussion

FA content

The FA biomarkers indicated that the relative amounts of diatoms, dinoflagellates, and bacteria in i-POM differed from those in p-POM and changed seasonally within p-POM. Although algal species were not identified in these samples, the algal class composition of POM can be partially inferred using FA biomarkers (reviewed in Dalsgaard et al. 2003). Using 16:4n-1 and the ratio of 16:1/16:0 as diatom biomarkers and the ratio of 22:6n-3/20:5n-3 as a dinoflagellate biomarker, i-POM during maximum ice extent appears to be dominated by diatoms, as is typical for Arctic sympagic communities (Horner 1985; Gradinger 2002; Arrigo et al. 2010). The ratios of the diatom marker 16:1/16:0 in the i-POM sampled during maximum ice extent, the *M. arctica* sampled during ice melt, and also the p-POM sampled during ice melt had similar values to those found in ice algae (2.7) and phytoplankton (2.3) from the Chukchi region (Budge et al. 2008). Additionally, the FA composition of the *M. arctica* sampled during ice melt confirmed that these FA ratios are a good diatom indicator in Arctic sea ice. In comparison, the ice algae sample from Budge et al. (2008), which was dominated by the pennate diatom *Navicula* sp., contained almost twice as much of the diatom marker 16:1n-7 (50.0 %) and approximately three times less of diatom markers 16:4n-1 (2.1 %) and 20:5n-3 (9.6 %) than our centric diatom *M. arctica* sample. Proportions of other FAs were similar between our *M. arctica* sample and the *Navicula* sp. samples from Budge et al. (2008). Different diatom species can produce different proportions of FA (i.e., Viso and Marty 1993, Dunstan et al. 1994). Thus, species differences may explain the striking differences in the three diatom markers (16:1n-7, 16:4n-1, and 20:5n-3) in the proportions of some FAs between our *M. arctica* sample and the *Navicula* sp. samples from Budge et al. (2008). Differences in environmental conditions between the Bering and Chukchi Seas at the time of sampling may have also contributed to the differences in FA profiles between these two diatom species as temperature, nutrient, and light availability are known to influence phytoplankton FA composition (Harrison et al. 1990; Thompson et al. 1992; Leu et al. 2010).

The relative abundance of diatom marker 16:4n-1 from p-POM taken during maximum ice extent was almost an order of a magnitude lower than that of i-POM, which could indicate lower diatom abundance in p-POM under heavy ice conditions or that concentrations of diatom FAs in p-POM were lower than in i-POM. The relative amounts of diatom markers 16:1/16:0 and 16:4n-1 for p-POM doubled in amount during ice melt compared with those measured during maximum ice extent. The presence of diatoms in p-POM during ice melt was confirmed by the observation of diatoms such as *Thalassiosira* sp., *N. frigida*, *Fragilariopsis* sp., *Chaetoceros* sp., and *Pseudonitzschia* sp., in these p-POM samples, with only three of 21 stations having notable amounts of the prymnesiophyte *Phaeocystis* (K. Iken, personal observation). Furthermore, the relative proportions of 16:0, 18:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 16:4n-1, 20:5n-3, and 22:6n-3 in p-POM during ice melt are very similar to those found in the pelagic phytoplankton samples from Budge et al. (2008), which comprised mainly of the large centric diatom *Coscinodiscus* sp. This similarity also suggests that the p-POM samples during ice melt contained diatoms. The diatom species present during maximum ice extent are unknown but the diatom marker FAs during that time was much lower than during ice melt. The relative amounts of diatom markers 16:1/16:0 and 16:4n-1 for p-POM were lowest during maximum ice extent and ice-free conditions, and highest during ice melt while the dinoflagellate indicator 22:6n-3/20:5n-3 showed the opposite pattern. This seasonal change in dominance of diatoms is consistent with a succession of taxa from low levels of primary production during maximum ice extent limited by light and stratification, transitioning to a water column seeded by diatoms released from sea ice as it melted during a spring bloom (McRoy and Goering 1974; Alexander and Niebauer 1981; Jin et al. 2007). When the ice retreats in the Bering Sea, the diatom bloom community can be succeeded by non-diatom phytoplankton such as dinoflagellates, haptophytes such as *Phaeocystis* sp., and *Synechococcus* sp., and *cryptophytes* (Moran et al. 2012). Although 22:6n-3/20:5n-3 has been historically used as a dinoflagellate indicator because 22:6n-3 can be produced in large amounts by dinoflagellates, 22:6n-3 can also be biosynthesized by heterotrophic flagellates (e.g., Desvilettes and Bec 2009, Bec et al. 2010). Therefore, it is possible that an increase in 22:6n-3/20:5n-3 of p-POM from ice melt to ice-free conditions may be due to a shift toward a stronger microbial food web with heterotrophic protists. The increased contribution of bacteria to p-POM is further supported by the increase in the bacterial biomarkers in the water column during ice melt to ice-free conditions (see below). Most likely the increase in 22:6n-3/20:5n-3 reflects a combination of increased dinoflagellate production with concurrent decreases in diatom production, as well as contributions from heterotrophic protists that can synthesize 22:6n-3 from other FA precursors such as 20:5n-3.

The proportion of bacterial FA markers indicates the presence of bacteria in POM, and the concentration of this marker suggests a greater total abundance of bacteria in the bottom 1 cm of sea ice than in the water column. In fact, bacteria can contribute up to 50 % of the total biomass within sea ice (Gradinger and Zhang 1997) and can be up to 100 times greater in abundance in Arctic sea ice relative to the water column (Maranger et al. 1994). In comparison, the bacterial FA marker in ice algae from the Chukchi region (1.4 %) was lower than that found in i-POM during maximum ice extent and higher than the bacterial marker in *M. arctica*. The bacterial FA marker in pelagic phytoplankton from the Chukchi region (0.9 %) was lower than those in p-POM (1.8–3.6 %), indicating a higher relative contribution of bacteria in p-POM. In addition to algae and bacteria, the POM samples most likely contained small amounts of detritus and microzooplankton that may have influenced FA profiles of these samples. Within sea ice, meiofauna typically contribute a minor fraction to total biomass and heterotrophic flagellates can be an important source of carbon (Gradinger et al. 1999). However, the FA profiles of i-POM and p-POM (during ice melt) were similar to those found in pure ice algae and pelagic phytoplankton from the Chukchi Sea (Budge et al. 2008); therefore, the presence of material other than algae is likely negligible.

In addition to the differences and seasonal changes in community composition of POM in the Bering Sea, the nutritional quality (i.e., levels of PUFA) of POM within sea ice and the water column also varied, as well as seasonally within the water column. Seasonal increase of FA concentrations within the water column during ice melt could be explained by an increase of phytoplankton cells during the spring bloom or from ice algae being released into the water column. The diatom FA biomarkers 16:1/16:0 and 16:4n-1 suggest that the increases in relative proportions of FAs in p-POM during ice melt are largely from the release of i-POM. However, if p-POM during ice melt was largely influenced by sinking i-POM we might expect the $\delta^{13}C_{FA}$ of p-POM to be similar to that of i-POM, but this is not the case. It is likely that the p-POM during ice melt is influenced by both the sinking of i-POM and active p-POM production in the water column. The concentrations of n-3 and n-6 PUFA in the bottom 1 cm of sea ice ranged from 40 to almost 300 times greater than those measured in the water column. The higher PUFA levels in sea ice compared to the water column indicated that the material in the bottom 1 cm of sea ice has a higher, concentrated, nutritional value than that of material in the water column, likely making the sea ice habitat an important, concentrated source of PUFA for grazers (e.g., Falk-Petersen et al. 1998) and presumably for higher trophic levels (e.g., Bluhm et al. 2010). For example, the Arctic bivalve *Macoma balthica* preferentially consumed sea ice algae over phytoplankton, and both *M. balthica* and the amphipod *Monoporeia affinis* had higher levels of

PUFA and total FAs when fed on sea ice algae compared to phytoplankton (Sun et al. 2009). Thus, these two Arctic benthic species may provide an important source of PUFA for animals that consume them. A similar observation was noted in the copepod *Calanus glacialis* in Rijpfjorden, Svalbard, Norway where its FA composition indicated that sea ice algae were an important food source during the spring bloom, when ice algae, not pelagic algae, triggered the reproduction of zooplankton (Leu et al. 2011). It may be that sea ice algae are preferentially eaten by some consumer taxa simply because they are present in larger concentrations than phytoplankton when released from the sea ice (e.g., Carroll and Carroll 2003). However, higher ice algal concentrations would also provide greater concentrations of PUFA to consumers.

$\delta^{13}C_{FA}$ values

In addition to differences in FA profiles between i-POM and p-POM, and variances in the nutritional content between sea ice and the water column, our data suggest that there are fundamental differences in the processes influencing FA production in the sympagic versus pelagic habitat. Overall, most of the 13 FAs from i-POM analyzed for their $\delta^{13}C$ were more enriched in ^{13}C compared to p-POM, including the diatom biomarkers 16:4n-1 and 20:5n-3. These results agree with some previous bulk and compound-specific carbon stable isotope analyses of sea ice algae and i-POM that have shown them to be more enriched in ^{13}C than pelagic phytoplankton and p-POM (Hobson et al. 1995; Gibson et al. 1999; Søreide et al. 2006, 2013; Budge et al. 2008; Tamelander et al. 2008). This implies that isotopic reaction processes during FA production differ markedly between the sympagic and pelagic environments in which the FAs were synthesized. The i-POM $\delta^{13}C_{FA}$ values increased with increasing day length, while the $\delta^{13}C_{FA}$ values from p-POM generally showed relatively little variation with increasing light availability during the same sampling period. We suggest that these patterns are consistent with a substantial influence of the photosynthetic isotope effect on FA production of i-POM from a limited DIC substrate within the semi-closed/closed sympagic system (Kennedy et al. 2002; Papadimitriou et al. 2007). These relatively higher photosynthetic demands within sea ice force decreased ^{13}C discrimination during photosynthesis and the subsequent increase in $\delta^{13}C_{FA}$ values in sympagic FAs, while pelagic production can draw from a constantly renewed DIC pool.

Patterns observed in $\delta^{13}C_{FA}$ values with increasing day length in the two POM types during maximum ice extent allow reaction progress associated with FA synthesis in sea ice to be inferred. Firstly, the $\delta^{13}C_{FA}$ values for many of the FAs of i-POM and p-POM were similar at the lowest day length, which is an indication of the baseline

fractionation associated with FA synthesis relative to source DIC. Secondly, the $\delta^{13}C_{FA}$ values of p-POM FAs were relatively invariable over the light availability gradient, which is consistent with FA synthesis by primary production in an open system where source DIC is constantly being replenished. Thirdly, bulk $\delta^{13}C$ values measured in i-POM increased, as did the $\delta^{13}C_{FA}$ values for many of the sympagic FAs, with increased light availability, which is consistent with a reaction progress in a closed system (e.g., Fry 2006). Finally, the $\delta^{13}C_{FA}$ values of many of the sympagic FAs differed under the highest light conditions relative to typical marine DIC values, which implies that the fraction of the source reacted increased with increasing day length, but reaction progress did not go to completion. In other words, when the reaction progress is complete, the $\delta^{13}C_{FA}$ value of i-POM should equal that of the initial $\delta^{13}C$ value of source DIC (Fry 2006). The estimated 12–73 % of source DIC reacted indicated that in the semi-closed/closed sea ice system, DIC was not completely limiting and was still available for FA synthesis.

There are many factors that, in combination, contribute to the variability in our estimates of reaction progress among sympagic FAs. One source of variability could be that synthesis pathways may be different for the various FAs analyzed. On average, SAT and PUFA gave similar estimates of reaction progress (51 and 50 %, respectively) while, overall, MUFA gave a higher estimate of reaction progress (64 %). This may reflect the activities of different desaturase enzymes used to insert bonds versus elongation enzymes used to add carbon to FAs. Another source of variability in reaction progress estimates could stem from the $\delta^{13}C$ values for surface water DIC. The $\delta^{13}C$ values for surface water DIC in the Bering Sea are not available, therefore, we used values estimated for the entire Pacific Ocean and also from the Gulf of Alaska (Gruber et al. 1999; Quay et al. 2003), which may not reflect the true value for our study area. However, the range of source DIC $\delta^{13}C$ values we used provided very similar estimates of fraction of source DIC reacted. We suggest that additional factors besides day length may also influence reaction progress estimates for sympagic FA synthesis (i.e., nutrient availability, brine convection, internal carbon mineralization). An incomplete reaction progress could also be due to sampling time, i.e., day length at the time of sampling may not have been great enough. Replenishment of the DIC pool could also lead to an incomplete reaction progress. This could also occur from the recycling of carbon from the breakdown of organic matter within sea ice and if the sympagic system was a semi- rather than a fully closed system. The most parsimonious explanation is that ice breakup occurs before the reaction of DIC can go to completion, and there is insufficient time to exhaust the DIC pool within sea ice. Further research is needed to determine if $\delta^{13}C_{FA}$ values of POM vary regionally and annually, and what factors may influence reaction progress estimates for sympagic FA synthesis.

Conclusion

In summary, we found differences in FA profiles and $\delta^{13}C_{FA}$ values between i-POM and p-POM and seasonally within p-POM. We demonstrated that these results can be explained as differences and changes in the composition of diatoms, flagellates, and bacteria using FA biomarkers. Concentrations of FA within the bottom 1 cm of sea ice were much greater than those found in the water column, making the sea ice a concentrated source of PUFA for marine grazers. In i-POM, the FAs became more enriched in ^{13}C with increasing day length, and we suggest that the decreased isotopic discrimination during photosynthesis in the carbon-limited and semi-closed sympagic habitat influences this pattern. Finally, we estimated that between 12 and 73 % of sea water DIC was used for FA synthesis in i-POM.

The marked differences in diatom versus flagellate composition in sympagic and pelagic community POM in 2010 and the higher nutritional content within the bottom 1 cm of sea ice compared to within the water column may have implications for marine grazers and possibly higher trophic levels. Of the regions in the Arctic and sub-Arctic, the Bering Sea exhibits the largest seasonal sea ice advance and retreat (Walsh and Johnson 1979; Niebauer 1983; Minobe 2002; Bluhm and Gradinger 2008). By 2050, the spring sea ice extent in the eastern Bering Sea is predicted to be 58 % of the 1980–1999 mean (Wang et al. 2012). As a result of this overall loss of sea ice and early ice retreat due to climate change, a reduction of sea ice primary productivity is predicted to occur (e.g., Bluhm and Gradinger 2008). Additionally, climate-related changes in the timing of seasonal sea ice cover affect spring primary production patterns (Stabeno et al. 2001, 2010; Hunt and Stabeno 2002). These changes in timing of sea ice retreat, predicted loss of sea ice and sea primary productivity, along with increased light intensities may lead to a reduction in high-quality PUFA from i-POM available for sympagic marine organisms and could have profound effects on ice-associated fauna, and possibly on upper trophic level consumers that rely on them as a food resource. The characteristics of FA in i-POM and differences from p-POM elucidated in our study will aid efforts to track the quantitative importance of sea ice algae FA to higher trophic levels in the Bering Sea.

Acknowledgments

This project was funded by the National Science Foundation (ARC-0902177 and 0732767). Financial support for S. Wang was also provided by the North Pacific Research Board Graduate Research Award, the University of Alaska Center (UAF) for Global Change Student Research Grant with funds from the Cooperative Institute for Alaska Research, Robert Byrd Award, Dieter Family Marine Science Research Scholarship, and the Ken Turner Memorial Fellowship. We thank J. Weems and S. Brennan (UAF) for assisting with sample collections and A. Timmins (Dalhousie) for laboratory assistance. We also thank T. Howe, N. Haubenstock, C. Graham from the ASIF-UAF for laboratory assistance with stable isotope analyses. We are grateful for the excellent assistance of the crew and captains of the USCGC Polar Sea and the UNOLS vessel Thomas G. Thompson, and chief scientists L. Cooper (University of Maryland Center for Environmental Science), C. Ashjian (Woods Hole Oceanographic Institution), and D. Shull (Western Washington University). We also thank E. Lessard (University of Washington) for assistance with phytoplankton identifications. Sea ice concentration data were sourced from the model explorer provided by the Alaska Ocean Observing System. Finally, we thank D. O'Brien, L. Horstmann-Dehn, A. Springer, and L. Oxtoby for helpful discussions and comments, and three anonymous reviewers for their detailed and constructive comments which improved our manuscript. Author Contributions: SWW wrote the manuscript. SWW performed the compound-specific stable isotope analysis and analyzed the data. MJW and SMB formulated the concept. SMB developed methodology and performed the fatty acid laboratory analysis. RRG and KI conducted fieldwork and provided editorial advice. RRG provided ideas for data analysis.

References

Abrajano TA, Murphy DE, Fang J, Comet P (1994) $^{13}C/^{12}C$ ratios in individual fatty acids of marine mytilids with and without bacterial symbionts. Org Geochem 21:611–617

Alexander V, Niebauer HJ (1981) Oceanography of the eastern Bering Sea ice-edge zone in spring. Limnol Oceanogr 26:1111–1125

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Aust Ecol 26:32-46

Arrigo KR, Mock T, Lizotte MP (2010) Primary producers and sea ice. In: Thomas DN, Dieckmann GS (eds) Sea ice. Wiley-Blackwell, Oxford, pp 283–325

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374–383

Bec A, Martin-Creuzburg D, Von Elert E (2010) Fatty acid composition of the heterotrophic nanoflagellate *Paraphysomonas* sp.: influence of diet and de novo biosynthesis. Aquat Biol 9(107):112

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18:S77–S96

Bluhm BA, Gradinger RR, Schnack-Schiel SB (2010) Sea ice meio and macrofauna. In: Thomas DN, Dieckmann GS (eds) Sea ice. Wiley-Blackwell, Oxford, pp 357–393

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29:1547–1559

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mammal Sci 22:759–801

Budge SM, Springer AM, Iverson SJ, Sheffield G (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. Mar Ecol Prog Ser 336:305–309

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an Arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117–129

Carroll ML, Carroll J (2003) The Arctic seas. In: Black KD, Shimmield GB (eds) Biogeochemistry of marine systems. CRC, Boca Raton, pp 127–156

Cavalieri DJ, Parkinson CL, Gloersen P, Zwally H (1996, updated yearly) Sea ice concentrations from Nimbus-7 SMMR and DMSP SSMI/I-SSMIS passive microwave data. 2010. NASA DAAC at the National Snow and Ice Data Center, Boulder, CO

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Claustre H, Marty J-C, Cassiani L, Dagaut J (1988/1989) Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications. Mar Microb Food Webs 3:51–66

Cooper LW, Sexson MG, Grebmeier JM, Gradinger R, Mordy CW, Lovvorn JR (2013) Linkages between sea-ice coverage, pelagic–benthic coupling, and the distribution of spectacled eiders: Observations in March 2008, 2009 and 2010, northern Bering Sea. Deep Sea Res II (in press)

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Dehn L-A, Sheffield G, Follmann E, Duffy L, Thomas D, O'Hara T (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167–181 Oecologia (2014) 174:699–712 711

Desvilettes C, Bec A (2009) Formation and transfer of fatty acids in aquatic microbial food webs: role of heterotrophic protists. In: Arts MT, Brett MT, Kainz MJ (eds) Lipids in aquatic ecosystems. Springer, New York, pp 25–42

Dunstan GA, Volkman JK, Barrett SM, Leroi JM, Jeffrey SW (1994) Essential polyunsaturated fatty acids from 14 species of diatom (*Bacillariophyceae*). Phytochem 35:155–161

Falk-Petersen S, Sargent JR, Henderson J, Hegseth EN, Hop H, Okolodkov YB (1998) Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. Polar Biol 20:41–47

Feder H, Iken K, Blanchard A, Jewett S, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using $\delta^{13}C$ and $\delta^{15}N$ analyses. Polar Biol 34:521–532

Fischer G (1991) Stable carbon isotope ratios of plankton carbon and sinking organic matter from the Atlantic sector of the Southern Ocean. Mar Chem 35:581–596

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509

Fry B (2006) Technical supplement 7B: derivations of closed system isotope equations. Stable isotope ecology. Springer, New York

Gibson JAE, Trull T, Nichols PD, Summons RE, McMinn A (1999) Sedimentation of ^{13}C-rich organic matter from Antarctic sea-ice algae: a potential indicator of past sea-ice extent. Geology 27:331–334

Gradinger RR (2002) Sea ice microorganisms. In: Bitten G (ed) Encyclopedia of environmental microbiology. Wiley, Hoboken, pp 2833–2844

Gradinger R, Zhang Q (1997) Vertical distribution of bacteria in Arctic sea ice from the Barents and Laptev Seas. Polar Biol 17:448–454

Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep Sea Res II 46:1457–1472

Gradinger RR, Kaufman MR, Bluhm BA (2009) Pivotal role of sea ice sediments in the seasonal development of near-shore Arctic fast ice biota. Mar Ecol Prog Ser 394:49–63

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annu Rev Mar Sci 4:63–78

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461–1464

Gruber N, Keeling CD, Bacastow RB, Guenther PR, Lueker TJ, Wahlen M, Meijer HAJ, Mook WG, Stocker TF (1999) Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic suess effect. Global Biogeochem Cycles 13:307–335

Harrison PJ, Thompson PA, Calderwood GS (1990) Effects of nutrients and light limitation on the biochemical composition of phytoplankton. J Appl Phycol 2:45–56

Hobson K, Ambrose WJ, Renaud P (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from δ^{13}C and δ^{15}N analysis. Mar Ecol Prog Ser 128:1–10

Horner RA (1985) Taxonomy of sea ice microalgae. In: Horner RA (ed) Sea ice biota. CRC, Boca Raton, pp 147–158

Hunt GL, Stabeno PJ (2002) Climate change and the control of energy flow in the southeastern Bering Sea. Prog Oceanogr 55:5–22

Hunt GL Jr, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Res II 49:5821–5853

Hunt GL, Coyle KO, Eisner LB, Farley EV, Heintz RA, Mueter F, Napp JM, Overland JE, Ressler PH, Salo S, Stabeno PJ (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J Mar Sci 68:1230–1243

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res II 57:71–85

Jin MB, Deal C, Wang J, Alexander V, Gradinger R, Saitoh S, Iida T, Wan ZW, Stabeno P (2007) Ice-associated phytoplankton blooms in the southeastern Bering Sea. Geophys Res Lett 34:L06612

Kennedy H, Thomas DN, Kattner G, Haas C, Dieckmann GS (2002) Particulate organic matter in Antarctic summer sea ice: concentration and stable isotopic composition. Mar Ecol Prog Ser 238:1–13

Leu E, Wiktor J, Søreide JE, Berge J, Falk-Petersen S (2010) Increased irradiance reduces food quality of sea ice algae. Mar Ecol Prog Ser 411:49–60

Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Prog Oceanogr 90:18–32

Lewis RW (1969) The fatty acid composition of Arctic marine phytoplankton and zooplankton with special reference to minor acids. Limnol Oceanogr 14:35–40

Litzow MA, Bailey KM, Prahl FG, Heintz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Mar Ecol Prog Ser 315:1–11

Maranger R, Bird DF, Juniper SK (1994) Viral and bacterial dynamics in Arctic sea ice during the spring algal bloom near Resolute, N.W.T., Canada. Mar Ecol Prog Ser 111:121–127

Mayzaud P, Chanut JP, Ackman RG (1989) Seasonal changes of the biochemical composition of marine particulate matter with special reference to fatty acids and sterols. Mar Ecol Prog Ser 56:189–204

Mayzaud P, Boutoute M, Noyon M, Narcy F, Gasparini S (2013) Lipid and fatty acids in naturally occurring particulate matter during spring and summer in a high Arctic fjord (Kongsfjorden, Svalbard). Mar Biol 160:383–398

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

McRoy CP, Goering JJ (1974) The influence of ice on the primary productivity of the Bering Sea. In: Hood DW, Kelley EJ (eds) Oceanography of the Bering Sea with emphasis on renewable resources. University of Alaska Fairbanks, Fairbanks, pp 403–421

McRoy CP, Goering JJ (1976) Annual budget of primary production in the Bering Sea. Mar Sci Commun 2:266–267

Minobe S (2002) Interannual to interdecadal changes in the Bering Sea and concurrent 1998/99 changes over the North Pacific. Prog Oceanogr 55:45–64

Moran SB, Lomas MW, Kelly RP, Gradinger R, Iken K, Mathis JT (2012) Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea. Deep Sea Res II 65–70:84–97

Naidu AS, Cooper LW, Finney BP, Macdonald RW, Alexander C, Semiletov IP (2000) Organic carbon isotope ratios ($\delta^{13}C$) of Arctic Amerasian Continental shelf sediments. Int J Earth Sci 89:522–532

Niebauer HJ (1983) Multiyear sea ice variability in the eastern Bering Sea—an update. J Geophys Res Oceans Atmos 88:2733–2742

Papadimitriou S, Thomas DN, Kennedy H (2007) Biogeochemical composition of natural sea ice brines from the Weddell Sea during early austral summer. Limnol Oceanogr 52: 1809–1823

Parrish CC (1999) Determination of total lipid, lipid classes and fatty acids in aquatic samples. In: Arts MT, Wainman BC (eds) Lipids in freshwater ecosystems. Springer, New York, pp 4–12

Peters J, Tuschling K, Brandt A (2004) Zooplankton in the Arctic Laptev Sea—feeding ecology as indicated by fatty acid composition. J Plankton Res 26:227–234

Quay P, Sonnerup R, Westby T, Stutsman J, McNichol A (2003) Changes in the $^{13}C/^{12}C$ of dissolved inorganic carbon in the ocean as a tracer of anthropogenic CO2 uptake. Global Biogeochem Cycles 17:1004

Reuss N, Poulsen L (2002) Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar Biol 141:423–434

Richter-Menge J, Overland J (2010) Arctic report card 2010. http://www.arctic.noaa.gov/report10

Rieley G (1994) Derivatization of organic compounds prior to gas chromatographic-combustion-isotope ratio mass spectrometric analysis: identification of isotope fractionation processes. Analyst 119:915–919

Schubert CJ, Calvert SE (2001) Nitrogen and carbon isotopic composition of marine and terrestrial organic matter in Arctic Ocean sediments: implications for nutrient utilization and organic matter composition. Deep Sea Res I 48:789–810

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59–87

Søreide JE, Carroll ML, Hop H, Ambrose WG, Hegseth EN, Falk-Petersen S (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopicand fatty acid tracers. Mar Biol Res 9:831–850

Stabeno PJ, Bond NA , Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the south-eastern Bering Sea. Fish Oceanogr 10:81–98

Stabeno P, Napp J, Mordy C, Whitledge T (2010) Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: sea ice, tides and winds. Prog Oceanogr 85:180–196

Sun M-Y, Clough LM, Carroll ML, Dai J, Ambrose WG Jr, Lopez GR (2009) Different responses of two common Arctic macrobenthic species (*Macoma balthica* and *Monoporeia affinis*) to phytoplankton and ice algae: will climate change impacts be species specific? J Exp Mar Biol Ecol 376:110–121

Tamelander T, Reigstad M, Hop H, Carroll ML, Wassmann P (2008) Pelagic and sympagic contribution of organic matter to zooplankton and vertical export in the Barents Sea marginal ice zone. Deep Sea Res II 55:2330–2339

Thomas DN, Papadimitriou S, Michel C (2010) Biogeochemistry of sea ice. In: Thomas DN, Dieckmann GS (eds) Sea ice. Wiley-Blackwell, Oxford, pp 425–468

Thompson PA, Gou M, Harrison PJ, Whyte JNC (1992) Effects of variation in temperature. II. On the fatty acid composition of eight species of marine phytoplankton. J Physcol 28:488–497

Viso A, Marty J (1993) Fatty acids from 28 marine microalgae. Prog Lipid Res 32:1521–1533

Walsh JE, Johnson CM (1979) An analysis of Arctic sea ice fluctuations, 1953–77. J Phys Oceanogr 9:580–591

Walsh JJ, McRoy CP (1986) Ecosystem analysis in the southeastern Bering Sea. Cont Shelf Res 5:259–288

Wang M, Overland JE, Stabeno P (2012) Future climate of the Bering and Chukchi Seas projected by global climate models. Deep Sea Res II 65–70:46–57

Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430–431:32–42

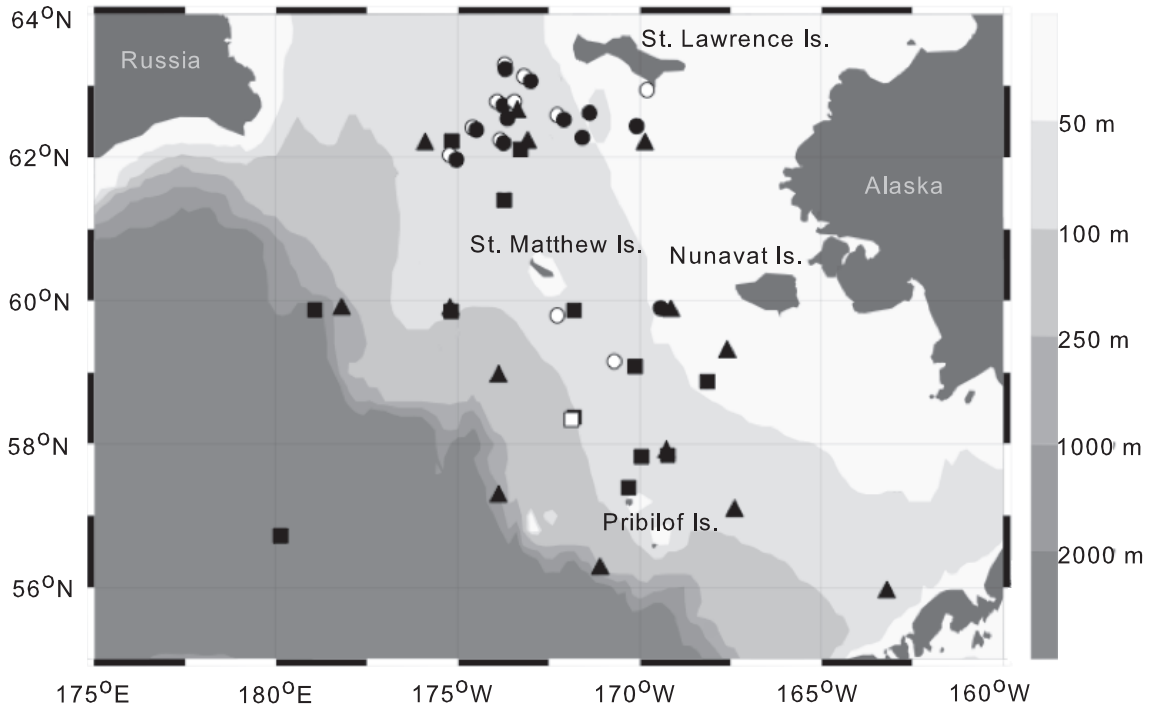


Figure 1.1 Sampling stations for i-POM and p-POM collected in the Bering Sea in 2010. i-POM = open symbols, p-POM = shaded symbols. Samples were collected during maximum ice extent 13–28 March (circles; i-POM *n* = 12, p-POM *n* = 14), ice melt between 11 May–10 June (squares; i-POM *n* = 1, p-POM *n* = 20), and ice-free (triangles; p-POM *n* = 15) conditions between 18 June and 10 July 2010. Ice conditions were based on the timing of sea ice conditions in the northern and central portions of the overall sampling area

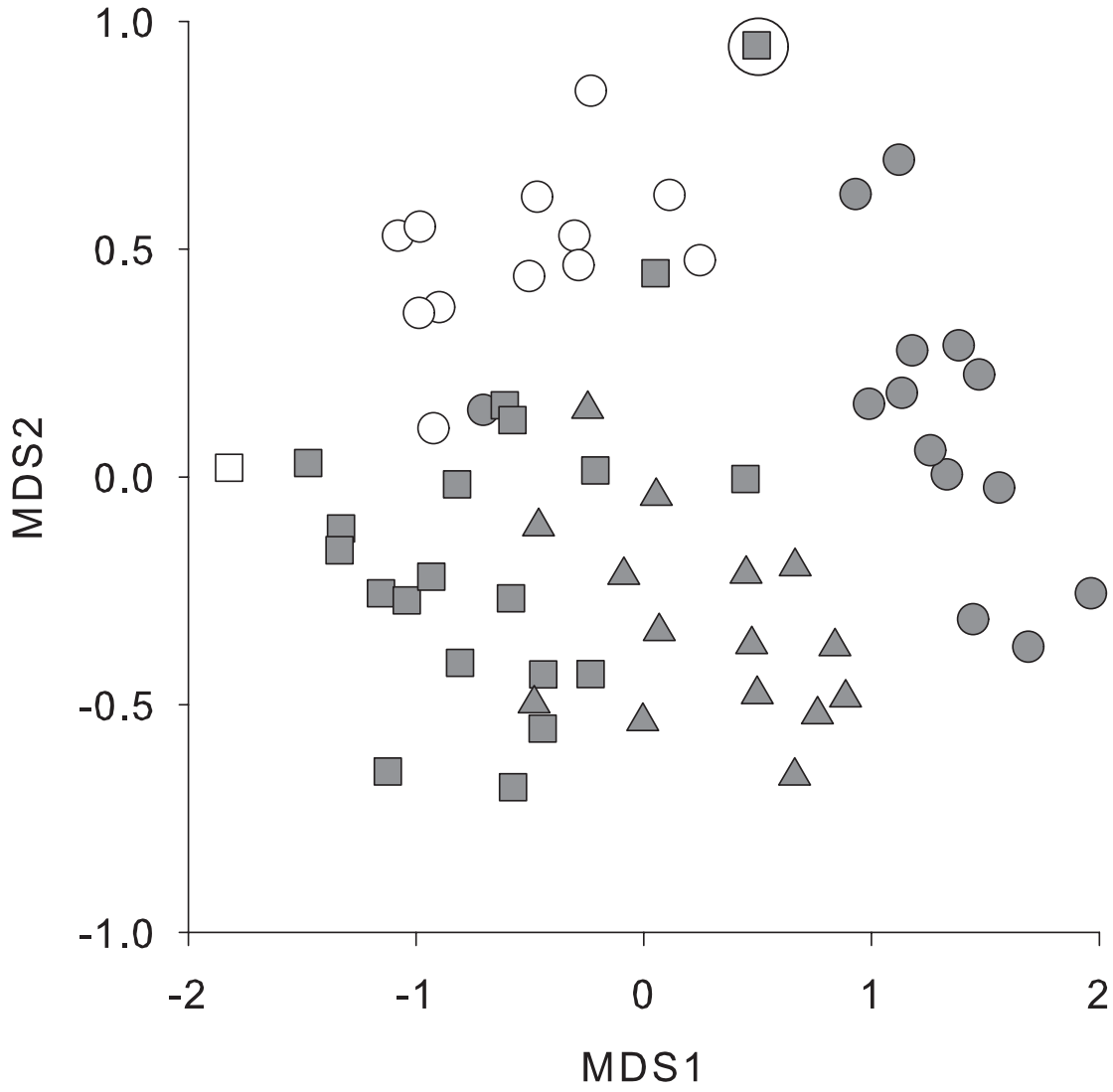


Figure 1.2 Non-metric multidimensional scaling (MDS) plot of i-POM and p-POM. i-POM = open symbols, p-POM = shaded symbols. Analysis used 59 fatty acids (FAs) present in proportions >0.1 % in samples collected in 2010 during maximum ice extent (circles; i-POM *n* = 12, p-POM *n* = 14), ice melt (squares; i-POM *n* = 1, p-POM *n* = 20), and ice-free (triangles; p-POM *n* = 15) conditions from all stations; data from the deep basin station are circled (two-dimensional stress = 0.09). For other abbreviations, see Fig. 1.1

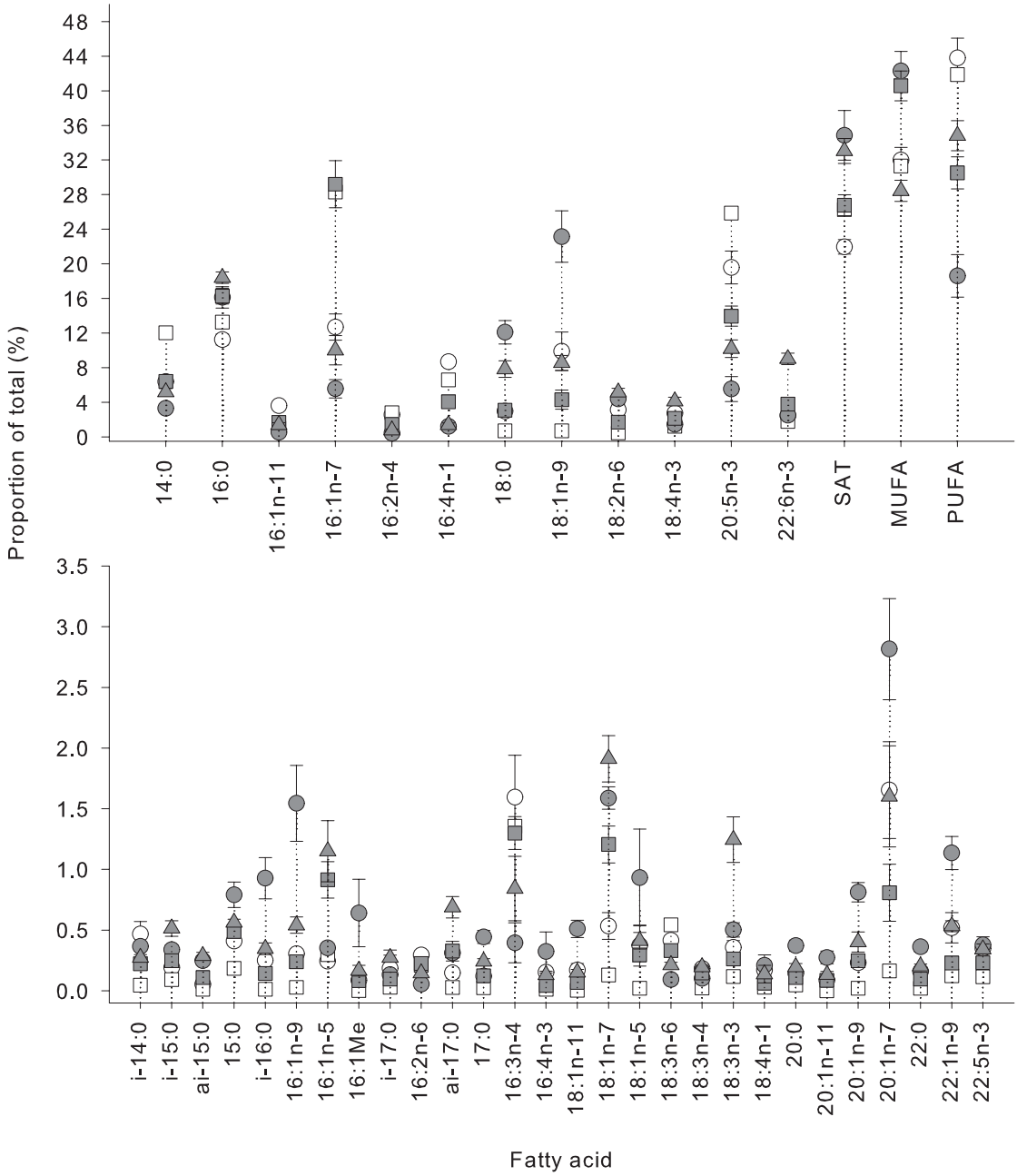


Figure 1.3 Proportions of some FAs (mean ± SE) in i-POM and p-POM. i-POM = open symbols, p-POM = shaded symbols. Samples collected in 2010 during maximum ice extent (circles; i-POM *n* = 12, p-POM *n* = 14), ice melt (squares; i-POM *n* = 1, p-POM *n* = 20), and ice-free (triangles; p-POM *n* = 15) conditions. For abbreviations, see Figs. 1.1 and 1.2

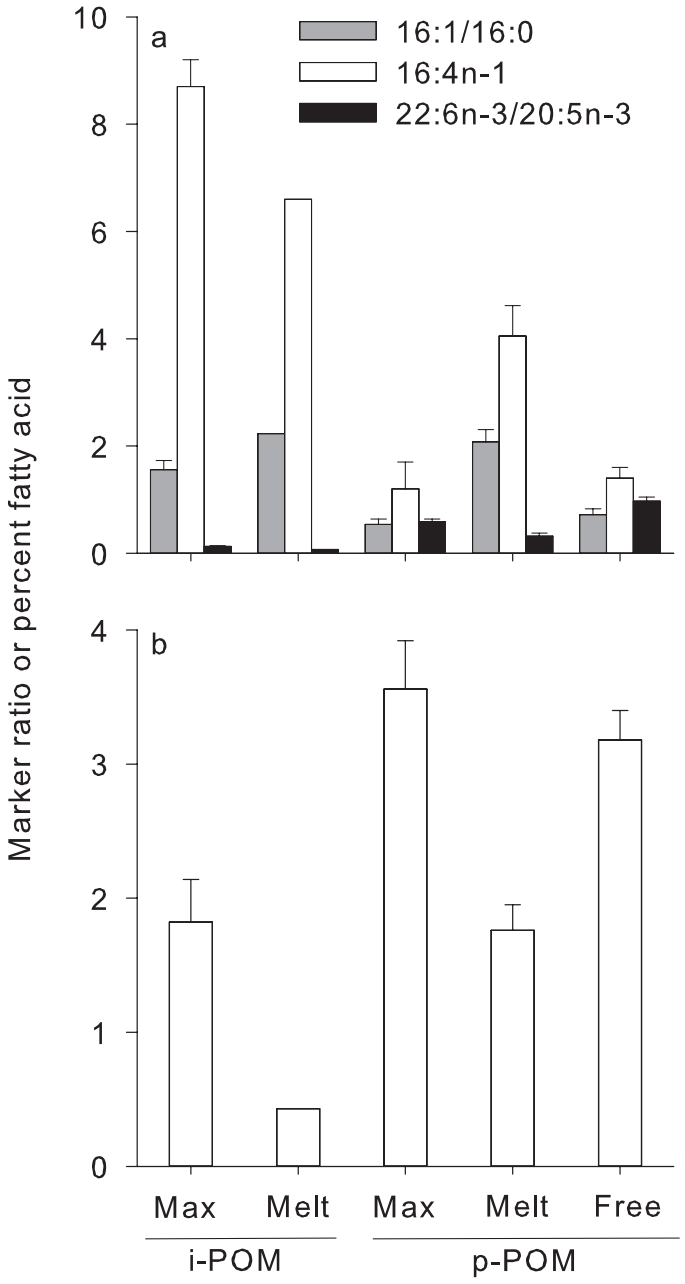


Figure 1.4 (a) Diatom FA indicators and dinoflagellate indicator and (b) bacterial FA indicator in i-POM and p-POM. Diatom FA indicators=16:1/16:0, 16:4n-1, dinoflagellate indicator=22:6n-3/20:5n-3, and bacterial FA indicator=sum of 15:0, 17:0 and all iso- and anteiso-branched chain FAs. Samples collected during maximum ice extent (Max; i-POM n = 12, p-POM n = 14), ice melt (Melt; i-POM n = 1, p-POM n = 20), and ice-free (Free; p-POM n = 15) conditions (mean ± SE). For other abbreviations, see Figs. 1.1 and 1.2

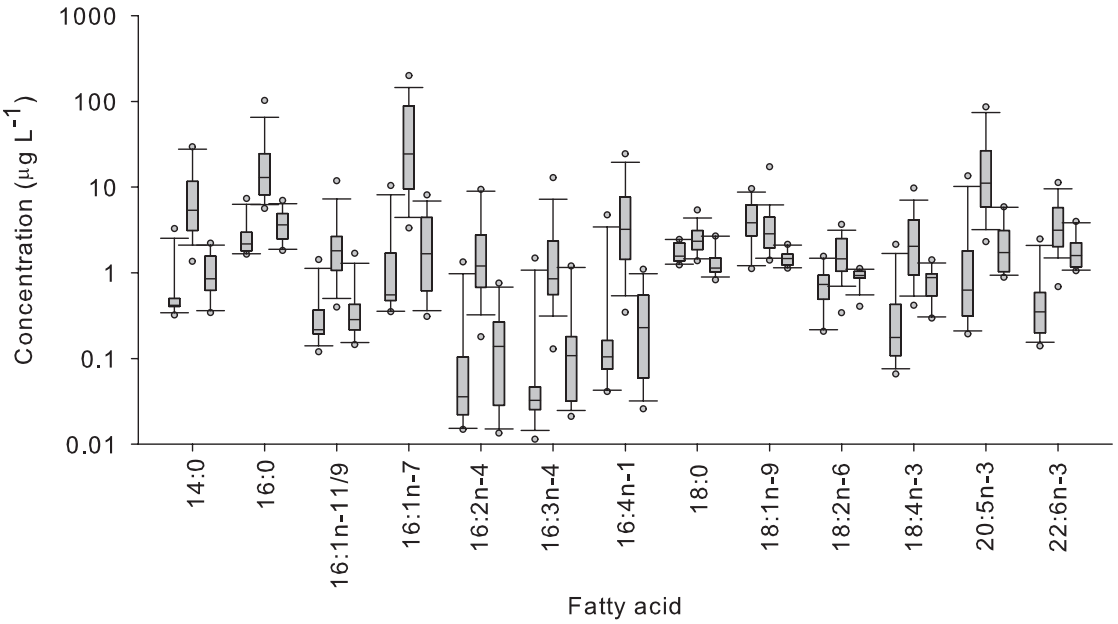


Figure 1.5 Boxplot of concentrations of 13 FAs in the water column. For each FA, the first boxplot represents maximum ice extent (n = 14), the second ice melt (n = 20), and the third ice-free conditions (n = 15). Ends of the boxes define the 25th and 75th percentiles, the line is at the median, the whiskers define the 10th and 90th percentiles, and the circles represent outliers. Note log scale used on y-axis

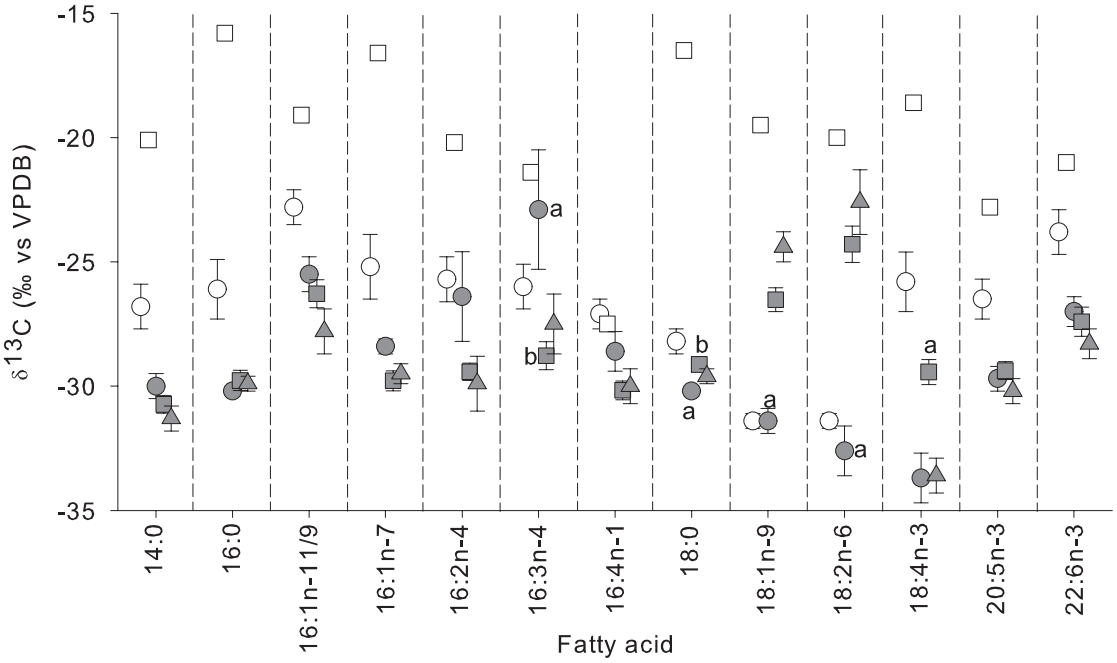


Figure 1.6 $\delta^{13}C_{FA}$ values for 13 select FAs (mean ± SE) in i-POM and p-POM. i-POM=open symbols and p-POM=shaded symbols. Samples were collected during maximum ice extent (circles; i-POM n = 10–12, p-POM n = 3–12), ice melt (squares; i-POM n = 1, p-POM n = 14–20), and ice-free (triangles; p-POM n = 1–14) conditions in 2010. Sample sizes are given as ranges because not all FAs were present in sufficient quantities to be analyzed by gas chromatography–isotope ratio mass spectrometry in each sample. These 13 FAs were identified in the majority of the samples (63–100 %). Different letters indicate differences between values within p-POM (Kruskal–Wallis ANOVA, $P < 0.04$). VPDB Vienna Pee Dee Belemnite; for other abbreviations, see Figs. 1.1 and 1.2

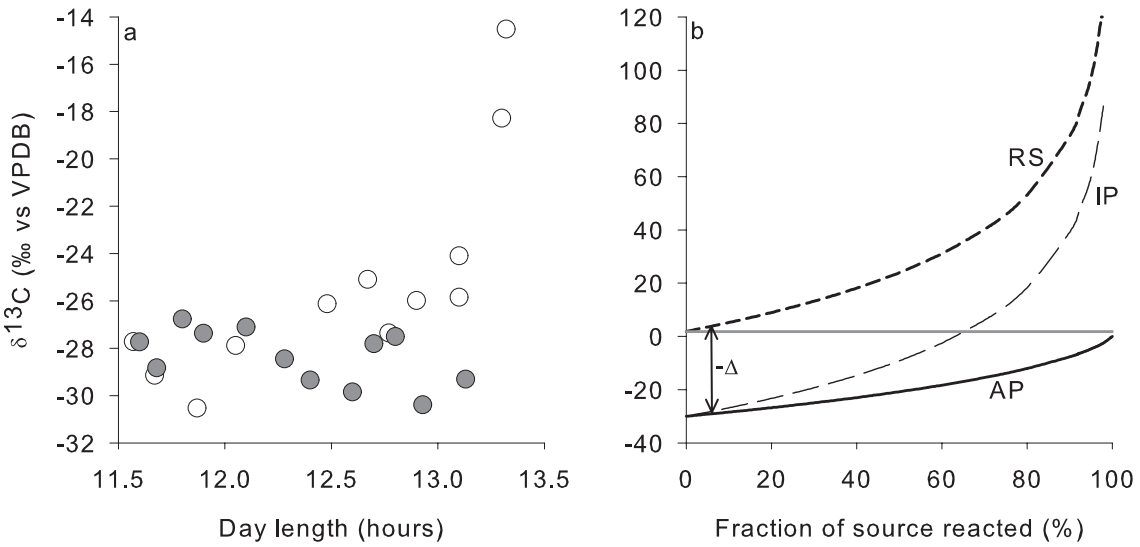


Figure 1.7 (a) Day length and $\delta^{13}C_{FA}$ values for FA 16:1n-7 in i-POM and p-POM, (b) isotopic fractionation (Δ) in a closed system. (a) i-POM=open symbols (n = 12) and p-POM=shaded symbols (n = 12). Samples collected during maximum ice extent conditions in 2010. Spearman's rank correlations for all other i-POM FAs and day length were significant except for 18:1n-9; (b) Δ is the difference between the residual substrate (RS) and instantaneous product (IP). In a closed system such as sea ice habitat, the source is ocean dissolved inorganic carbon [shaded horizontal line at 1.85 ‰ (Gruber et al. 1999)] and the accumulated product (AP) is measured i-POM. For other abbreviations, see Figs. 1.1, 1.2 and 1.6

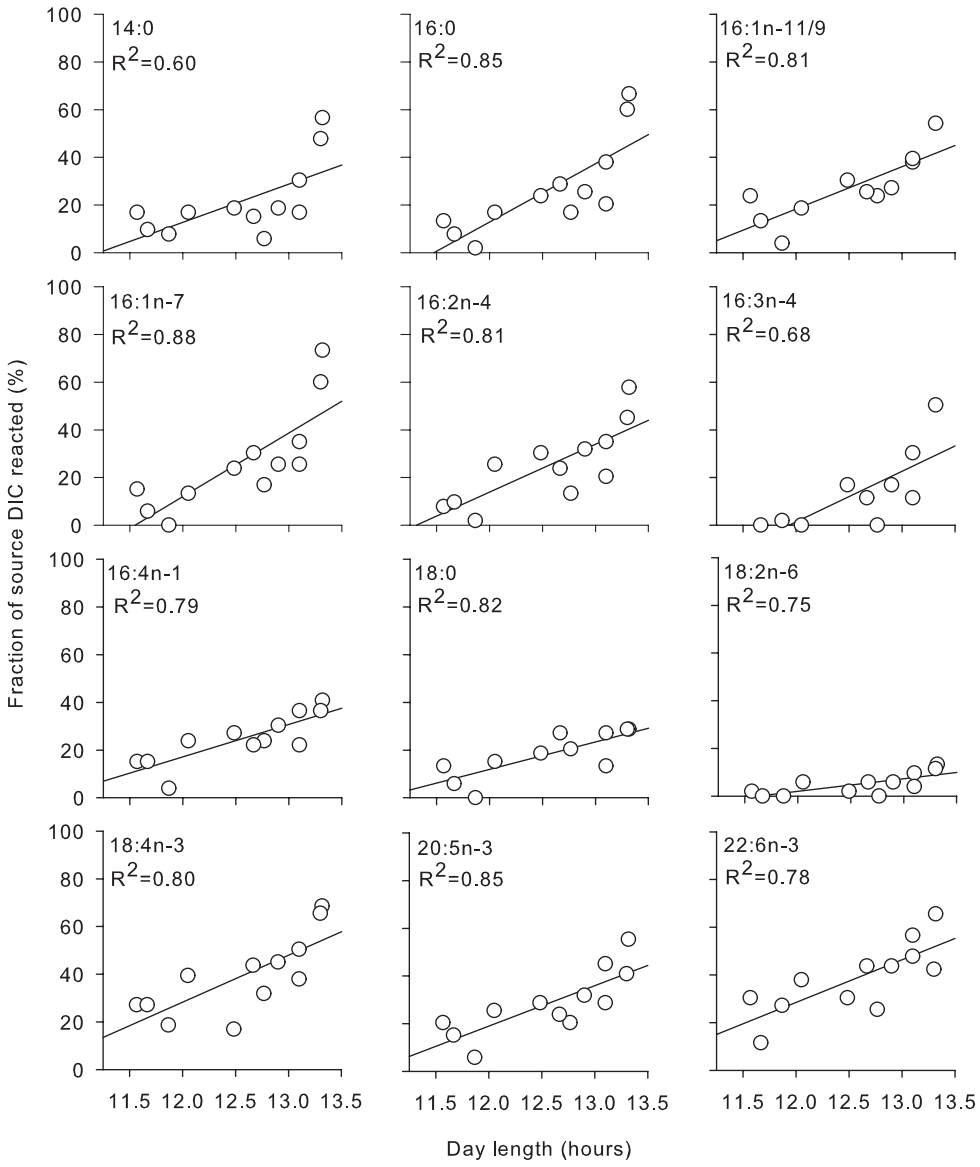
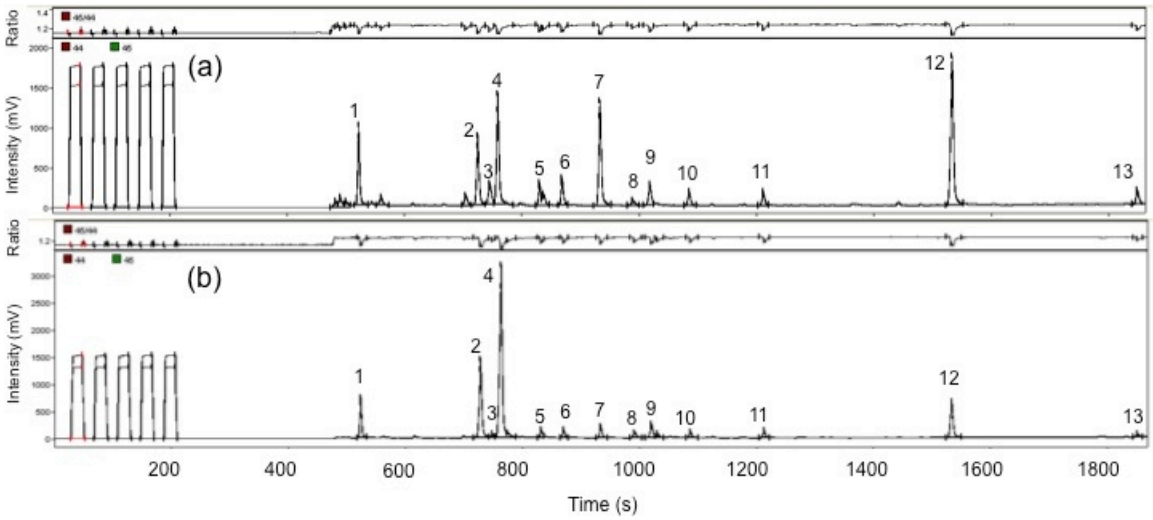


Figure 1.8 Day length and fraction of source dissolved inorganic carbon (DIC) reacted for 12 FAs of i-POM during maximum ice extent conditions in 2010. For all FA $n = 12$, except for 16:1n-11/9 ($n = 11$), 16:3n-4 ($n = 10$), and 18:0 ($n = 11$). Results shown for a source DIC value of 1.85 ‰ (Gruber et al. 1999). Results from using a value of 1.55 ‰ from Quay et al. (2003) gave similar results that could not be distinguished in the figure. Linear regressions were significant for all FA shown ($P < 0.02$). Data for 18:1n-9 not shown because they were not significant. For other abbreviations, see Figs. 1.1 and 1.2



Appendix 1.1 Sample GC-IRMS chromatogram traces for (a) i-POM and (b) p-POM from the Bering Sea. Peaks 1-13 are fatty acids 14:0, 16:0, 16:1n-11/9, 16:1n-7, 16:2n-4, 16:3n-4, 16:4n-1, 18:0, 18:1n-9, 18:2n-6, 18:4n-3, 20:5n-3 and 22:6n-3

approved

Rolf Gradinger
Associate Dean
School of Fisheries and Ocean Sciences
252 O Neill Building
Fairbanks AK 99775-7220

907 474 7407

http://www.sfos.uaf.edu/research/seaicebiota/
http://scholar.google.com/citations?user=1RKfeo0AAAAJ&hl=en

On 4/11/14 2:22 PM, Shiway Wang wrote:

> HI Rolf!
>
> Because you are not on my committee but are a coauthor, I need your permission to include the following papers in my dissertation:
>
> (Chapter 1) Wang SW, Budge SM, Gradinger RR, Iken K, Wooller (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699-712
>
> and
>
> (Chapter 2) Wang SW, Budge SM, Iken K, Gradinger RR, Wooller MJ. Zooplankton diets in the Bering Sea inferred using fatty acid and compound-specific stable isotope analyses reveal the relative importance of pelagic and sympagic carbon sources. In Review. Marine Ecology Progress Series
>
> Will you grant me permission to include these papers in my dissertation? :)
>
> thanks!
> Shiway
>
> --
> Shiway Wang
> MS Marine Biology
> PhD Candidate
> School of Fisheries & Ocean Sciences
> University of Alaska Fairbanks
> shiway@gmail.com
> (907) 460 2496
> https://www.sfos.uaf.edu/people/profile.php?uid=2160

Appendix 1.2 Permission to use manuscript in thesis from Rolf Gradinger

CHAPTER 2:

Zooplankton diets in the Bering Sea inferred using fatty acid and compound-specific stable isotope analyses reveal the relative importance of pelagic and sympagic carbon sources[1]

Abstract

We analyzed fatty acid (FA) profiles and carbon stable isotope compositions of individual FA ($\delta^{13}C_{FA}$) from three zooplankton species (*Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii*) sampled from the Bering Sea during maximum ice extent, ice melt, and ice-free conditions in 2009 and 2010. Our goal was to use FA and $\delta^{13}C_{FA}$ values of individual FA to assess zooplankton diets and estimate the proportional contribution of pelagic and sympagic sources to their diets. FA profiles showed little variation in diet within species between ice conditions or years, but revealed differences in diet among species. FA biomarkers confirmed that *T. libellula* was predominately carnivorous. In contrast, *C. marshallae/glacialis* and *T. raschii* were primarily herbivorous, consuming different proportions of water column and ice algal taxa, but displayed some degree of omnivory. Despite these inter-species differences in diets, estimates from four stable isotope mixing models using combinations of $\delta^{13}C_{FA}$ values of diatom FA markers (16:1n-7, 20:5n-3), and a flagellate FA marker (22:6n-3) showed that substantial, albeit highly variable, proportions of these FA originated from sea ice-derived organic matter (*T. libellula* 36–72%, *C. marshallae/glacialis* 27–63%, and *T. raschii* 39–71%). Our results suggest that these zooplankton species in the Bering Sea are linked, although not exclusively, to the sea ice algal community as a source of FA. Thus, depending on the timing of pelagic production relative to sympagic production and trophodynamic phasing, these zooplankton species may be more resilient to climate-induced changes at the base of the food web.

[1] Wang SW, Budge SM, Iken K, Gradinger RR, Springer AM, Wooller MJ. Zooplankton diets in the Bering Sea inferred using fatty acid and compound-specific stable isotope analyses reveal the relative importance of pelagic and sympagic carbon sources. In revision with Marine Ecology Progress Series

Introduction

Zooplankton, particularly crustaceans such as hyperiid amphipods, calanoid copepods, and euphausiids, are important prey for fishes, seabirds, and marine mammals in marine ecosystems and are thus key trophic links in the transfer of carbon and energy from primary producers to higher trophic levels. In the Bering Sea, prominent species include the hyperiid amphipod *Themisto libellula*, the copepods *Calanus glacialis* and *C. marshallae*, and the euphausiid *Thysanoessa raschii* (Frost & Lowry 1981, Springer & Roseneau 1985, Baier & Napp 2003, Ciannelli et al. 2004, Pinchuk et al. 2013, Strasburger et al. 2013). Although important as prey, the food sources of these species in the Bering Sea are not well known, but are thought to be similar to those in other high latitude seas (e.g., Pinchuk et al. 2013). *Themisto libellula* is considered to be predatory, with a diet in the North Atlantic that mainly consists of *Calanus* spp. copepodites (Marion et al. 2008, Noyon et al. 2009). *Calanus marshallae* and *C. glacialis* are predominately herbivorous but can be omnivorous (Smith 1990, Hobson et al. 2002, Sato et al. 2002, Baier & Napp 2003, Stevens et al. 2004a). *Thysanoessa raschii* is also primarily herbivorous but can also be carnivorous and may switch to detrital feeding during the winter (Mauchline & Fischer 1969, Falk-Petersen et al. 1981, Sargent & Falk-Petersen 1981, Smith 1991, Hagen & Auel 2001, Hop et al. 2006).

All of these species are known to have some degree of association with sea ice algae in seasonally ice-covered seas. For instance, fatty acid (FA) data from *T. libellula* indicate a strong linkage with sea ice algal production in the northern Fram Strait (Auel et al. 2002), and *C. glacialis* females graze on sea ice algae to support reproduction during the spring in the Canadian and European Arctic (e.g., Conover & Huntley 1991, Tourangeau & Runge 1991, Michel et al. 1996, Søreide et al. 2008). In the Bering Sea, *C. glacialis* feed on ice algal diatoms (*Fragilariopsis cynlindrus*, *Fragilaria* sp., and *Pseudonitzschia* sp.) and the release of ice algae in the water column supports the early reproduction of *C. glacialis* (Durbin & Casas 2014). Additionally, *C. marshallae* copepodite abundance was greatest in years of most southerly sea ice extent in the Bering Sea (Baier & Napp 2003), and *T. raschii* can be very abundant under sea ice in the Bering Sea and feeds on ice algae (Gradinger et al. unpublished). In the European Arctic, the contribution of carbon derived from sea ice algae to some zooplankton species (*Calanus finmarchicus*, *C. glacialis*, *Thysanoessa inermis*, *T. longicaudata*, *T. abyssorum*) was estimated to be as high as 50% (Søreide et al. 2006) and up to 70% in *Calanus* copepods (Søreide et al. 2008, 2013). In the Chukchi region off of Barrow, Alaska the contribution of sea ice algal carbon to *T. raschii* was estimated to be between 20–74% (Budge et al. 2008).

Climate warming in the Arctic and the associated loss of sea ice is predicted to alter the timing and quantity of primary production by pelagic phytoplankton and phytoplankton associated with sea ice (Stabeno et al. 2001, Hunt et al. 2002, Bluhm & Gradinger 2008, Stabeno et al. 2010, Brown & Arrigo 2012). Such changes in the food base may affect grazing zooplankton populations and upper trophic levels that depend on them for food (Grebmeier et al. 2006, Søreide et al. 2006, Bluhm & Gradinger 2008, Leu et al. 2011, Grebmeier 2012, Søreide et al. 2013). Understanding zooplankton foraging behavior and estimating the proportional contribution to zooplankton of carbon from sea ice algae versus that from pelagic algae will help predict how potential changes in primary production may affect the pelagic food web in the Bering Sea.

FA biomarkers have been used to determine sources of primary production (diatoms versus dinoflagellates) to zooplankton in Arctic Seas (Scott et al. 1999, Falk-Petersen et al. 2000, 2009, Scott et al. 2001, Hop et al. 2006, Søreide et al. 2008, 2013). Diatoms are high in the FA 16:1n-7, 16:4n-1, C16 polyunsaturated FA (PUFA), and 20:5n-3 (Viso & Marty 1993, Dunstan et al. 1994, Graeve et al. 1994). In comparison, dinoflagellates are high in C18 and C22 PUFA (e.g., Dalsgaard et al. 2003). C16 and C18 FA are found in elevated levels in diatoms and flagellates, respectively (e.g., Reuss & Poulsen 2002), however, the ratios of C16/C18 FA and 16:1/16:0 FA are high in diatoms compared to flagellates (Claustre et al. 1988-89, Viso & Marty 1993) and can be used to scale the relative importance of diatoms versus flagellates to zooplankton (e.g., Nelson et al. 2000, Søreide et al. 2008).

Along with describing herbivorous feeding, FA biomarkers have been used to infer levels of omnivory and carnivory in zooplankton. The FA 18:1n-9 is generally present in high levels in most marine animal lipids; thus, it has been used as a general marker of carnivory (Sargent & Falk-Petersen 1981, 1988, Falk-Petersen et al. 1990). The FA 18:1n-7 can be derived from the elongation of 16:1n-7, which is considered to originate from phytoplankton, and thus levels of these two FAs tend to reflect the extent of herbivory in zooplankton (Falk-Petersen et al. 2000). Consequently, the ratio of the FA 18:1n-9/18:1n-7 can be used to indicate levels of carnivory (Falk-Petersen et al. 1990, 2000, Graeve et al. 1997, Auel et al. 2002, Kürten et al. 2013). Long-chained C20 and C22 monounsaturated FAs (MUFA) are mainly biosynthesized by calanoid copepods (Sargent & Falk-Petersen 1988, Kattner & Hagen 1995, Lee et al. 2006) and can be used to indicate carnivory as well (e.g., Falk-Petersen et al. 1987).

FA biomarkers have also been used to detect the presence of sea ice algae in the diets of zooplankton (Scott et al. 1999, 2001). However, the same FA can characterize diatoms from sea ice and the water column; thus, using FA biomarkers alone to distinguish carbon sources (sea ice algae vs. phytoplankton) in zooplankton are often not

sufficient (i.e., Søreide et al. 2008). The carbon stable isotope values of specific FAs (expressed as $\delta^{13}C_{FA}$) in, e.g., 16:4n-1 and 20:5n-3, have been found to be relatively higher in particulate organic matter (POM) from sea ice (i-POM, assumed to consist primarily of ice algae) compared with pelagic-derived POM (p-POM, assumed to consist primarily of pelagic phytoplankton) (Wang et al. 2014). The $\delta^{13}C_{FA}$ values of sea ice algae were also found to be higher than in pelagic phytoplankton (Budge et al. 2008). These isotopic differences have been used to estimate the proportional contribution of sympagic (ice associated) and pelagic primary production to consumers in the Arctic (Budge et al. 2008, Graham et al. 2014).

Our goals in this study were to: (1) use FA biomarkers to describe the foraging strategies of the zooplankters *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii* in the Bering Sea and (2) compare $\delta^{13}C_{FA}$ values from these species with $\delta^{13}C_{FA}$ values of FA from i-POM and p-POM in the Bering Sea (Wang et al. 2014) to estimate the proportional contribution of i-POM and p-POM FA to them. We hypothesized that previously documented differences in the diet between *T. libellula*, *C. marshallae/glacialis*, and *T. raschii* would be supported by different FA profiles and biomarker compositions. We also hypothesized that the proportional contribution of i-POM FA would be highest in the primarily herbivorous *C. marshallae/glacialis* and *T. raschii* during maximum ice extent and decrease as the ice melted, and with the onset of the phytoplankton blooms in the water column. Similarly, the contribution of i-POM FAs in *T. libellula* would stem from their primary prey, *Calanus* copepods, and the estimates would vary in accordance with copepod availability.

Methods

Sample collection

Zooplankton were collected from the Bering Sea shelf as part of the Bering Sea Ecosystem Study/Bering Sea Integrated Ecosystem Research Program during three major seasonal ice regimes (maximum ice extent, ice melt, and ice-free conditions) in 2009 and 2010 in the northern and central portions of the Bering Sea (Fig. 2.1). In 2009, maximum ice extent occurred by 28 February and remained close to the maximum level through most of March (NSIDC 2009). In 2010, maximum ice extent occurred on 31 March (Richter-Menge & Overland 2010). Details for sampling stations are provided in Appendix 2.1. We examined three species: *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii*. *C. marshallae* and *C. glacialis* co-occur in the Bering Sea (Nelson et al. 2009) and could not be distinguished from one another on board; therefore, we refer to them as *Calanus*

marshallae/glacialis. Size and age class information for samples were not recorded for these samples. Zooplankton were collected using a ring net (mesh size 333 μm) hauled vertically from 10 m above the bottom, or a maximum of 150 m depth, to the surface. During ice-free conditions (cruises KNORR195 and TN250), zooplankton were collected from a 1 m2 Multiple Opening Closing Net and Environmental Sensing System (MOCNESS) fitted with 500 μm mesh and fished obliquely to a maximum of 150 m. Samples were stored in plastic microcentrifuge vials at -20°C until laboratory analysis.

POM samples in 2009 were collected on the Bering Sea shelf during ice melt conditions (Table 2.1). i-POM samples were obtained at varying depths from ice cores ranging from the bottom 1 cm section of the core to the bottom 4 cm of the core. Ice core samples were completely melted in the dark and filtered on pre-combusted GF/F filters. p-POM samples were collected from a single Niskin bottle closed at depths of 10 or 15 m below the surface. Samples were filtered using a GF/F filter (pore size 0.7 μm) and stored in chloroform at -20°C until laboratory analysis. Details for the collection of POM samples from 2010 were previously described by Wang et al. (2014).

Fatty acid analysis

Lipids were extracted from all samples using 2:1 chloroform/methanol (Folch et al. 1957, Parrish 1999). Individual plankters were pooled by species and station so that the combined samples contained on average 3.3 ± 3.4 (*T. libellula*), 17.6 ± 10.4 (*Calanus marshallae/glacialis*), and 4.1 ± 2.6 (*T. raschii*) individuals per sample (mean ± 1SD; see Appendix 2.1 for number of individuals per sample). Fatty acid methyl esters (FAME) were prepared using an acidic transesterification (Budge et al. 2006). Because fatty alcohols resulting from the transesterification of wax esters in zooplankton may co-elute with FAME when analyzed by GC, they were identified and removed from the samples using thin layer chromatography. FAME were quantified using temperature-programmed gas chromatography (GC) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30 m x 0.25 mm internal diameter column coated with 50% cyanopropyl- methylpolysiloxane (DB-23) and linked to a computerized integration system (Varian Star software). Shorthand nomenclature of A:Bn-X was used to describe each FAME, where A represents the number of carbon atoms, B the number of double bonds, n represents the terminal methyl group, and X the position of the double bond closest to the terminal methyl group. Approximately

70 FAME were identified by comparison of retention times with known standards (Nu Check Prep, Elysian, MN, USA), or using GC-mass spectrometry.

Carbon stable isotope analysis of individual fatty acids

Carbon stable isotope ratios of FAME samples (expressed as $\delta^{13}C$ values in per mil - ‰) were analyzed by routing the effluent from a GC (Trace GC Ultra, Bremen, Germany) through a combustion interface (Finnigan GC combustion III, Bremen, Germany) to an isotope ratio mass spectrometer (IRMS) (Thermo Finnigan Delta V, Bremen, Germany) at the Alaska Stable Isotope Facility (ASIF), University of Alaska Fairbanks (UAF). The same GC column and method described above for FID analyses of FAME were used to separate the FAME for analysis using GC-IRMS (Budge et al. 2008, Budge et al. 2011, Wang et al. 2014). The $\delta^{13}C$ values from the individual FAMEs were calibrated using a standard mixture consisting of ethyl and methyl esters of 14:0, 16:0, 18:0, and 20:0 (supplied by Indiana University Stable Isotope Reference Materials), where the coefficient of determination (r^2) of the measured versus expected relationship was >0.99. 16:0 and 18:0 FAME laboratory standards were analyzed after every ten samples to track analytical error of the GC-IRMS system, which was ≤0.3 ‰ (representing the 1 standard deviation-SD of 23 analyses of the 16:0 and 18:0 standards interspersed during the samples runs). All $\delta^{13}C$ values are reported relative to Vienna Pee Dee Belemnite (VPDB) using standard notation, where $\delta^{13}C$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$, and R is the corresponding ratio of $^{13}C/^{12}C$.

Data analysis

Bray-Curtis similarity matrices and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) were used to investigate the variation in FA compositions of zooplankton, based on the 63 FA present in proportions >0.1%, among species, and between years and ice conditions within species. Non-metric scaling (nMDS) plots were used to visualize differences between FA profiles among and within species. Similarity percentages routines (SIMPER) were performed to determine the FA contributing most to the observed differences among species and between years and ice conditions within species. FA data were standardized to 100% and log(1+X) transformed prior to analysis to downweight the FA present in higher proportions and increase the weighting of FA present in lower proportions.

We examined the proportions of FA biomarkers to assess the relative presence of bacteria, different algal taxonomic groups, and relative levels of carnivory in the three zooplankton species examined (e.g., Søreide et al. 2008, 2013). The sum of 15:0 and 17:0 FA, and the iso- and anteiso FA (i-14:0, i-15:0, ai-15:0, i-16:0, i-17:0, and ai-17:0) were used to determine the proportion of bacterial FA in the samples (Budge & Parrish 1998). The relative proportions of diatoms to flagellates in zooplankton diet were determined using the ratios of 16:1/16:0 and ΣC16/ΣC18 FA (Claustre et al. 1988/1989, Viso & Marty 1993). Relative levels of carnivory were determined from the ratios of 18:1n-9/18:1n-7 (Falk-Petersen et al. 1990, 2009, Graeve et al. 1997, Auel et al. 2002, Kürten et al. 2013) and PUFA/saturated FA (SFA) (Cripps & Atkinson 2000). The ratio of FA 20:5n-3/22:6n-3 was used to determine the proportion of diatoms to flagellates in zooplankton diets (Budge & Parrish 1998, Dalsgaard et al. 2003). The sum of C20 and C22 monounsaturated FA (MUFA) was used to determine the presence of *Calanus* copepods in the diet of zooplankton (Falk-Petersen et al. 1987, 2002, Søreide et al. 2013). A Kruskal–Wallis ANOVA was used followed by Bonferroni adjustment for multiple comparisons to test for differences in FA biomarkers among zooplankton species. ANOVA was performed using Statistica v12 (StatSoft, Inc.).

Not all FA were present in sufficient quantities to determine their respective $\delta^{13}C_{FA}$ values. $\delta^{13}C_{FA}$ values were determined for 16:0, 16:1n-7, 18:1n-11/9, 20:1n-11/9, 20:5n-3, and 22:6n-3 in all samples. The $\delta^{13}C_{FA}$ values for these six FA were transformed into Euclidean distances, and a PERMANOVA was used to investigate the variation in the $\delta^{13}C_{FA}$ values among species, and inter-annual and seasonal variation within species. PERMANOVA, SIMPER, and nMDS data analyses were performed in PRIMER v6 (Primer-E Ltd).

We used Bayesian multi-source stable isotope mixing models (SIAR, Parnell et al. 2010) to estimate the proportional contribution of i-POM relative to p-POM in zooplankton. The SIAR model incorporates the isotope values of consumers and representative sources of diet (end member sources) as well as trophic enrichment factors and concentration dependencies to produce estimates of the proportion of given diet items in consumers (Parnell et al. 2010). The model employs Bayesian statistics, which allows for incorporation of uncertainty and variation of isotope data to give a 95% credibility interval that includes the probability distribution of the estimates (Parnell et al. 2010). Although it is ideal to add trophic enrichment factors into the model to account for tissue specific isotopic turnover rates of consumers, no data exist for isotopic turnover of $\delta^{13}C_{FA}$ in zooplankton. Thus, trophic enrichment factors were assumed to be zero (Budge et al. 2008, 2011) and the consequences are explored in the Discussion. Models were run with and without concentration dependencies for comparison (Table 2.4). The $\delta^{13}C_{FA}$ values for i-

POM and p-POM were generated from many of the same sampling locations from which zooplankton were taken in 2009 (Fig. 2.1) and 2010 (Wang et al. 2014) and were used as the end member sources in our mixing models. Specifically, for zooplankton in 2009, average i-POM and p-POM $\delta^{13}C_{FA}$ values from samples collected during ice melt were used as sources in the mixing models for zooplankton collected in all ice conditions. In 2010, the average i-POM $\delta^{13}C_{FA}$ value from samples collected during maximum ice extent was used as the i-POM source and p-POM was collected from all three ice conditions, and their $\delta^{13}C_{FA}$ values were used to model their respective zooplankton samples (i.e., p-POM from ice-free conditions used as the p-POM source for zooplankton collected during ice-free conditions). The $\delta^{13}C_{FA}$ values for i-POM and p-POM are given in Table 2.2. A non-parametric Mann-Whitney U test was performed using Statistica v12 (StatSoft, Inc.) to assess differences in $\delta^{13}C_{FA}$ values of FA 16:1n-7, 20:5n-3, and 22:6n-3 between i-POM and p-POM in 2009. We used the diatom marker FA 16:1n-7 and 20:5n-3 in the model because the algal composition in i-POM is typically dominated by diatoms (Horner 1985, Gradinger 2002, Arrigo et al. 2010). The presence of diatoms was also found in p-POM in 2010 (Wang et al. 2014). We also used the flagellate marker 22:6n-3 in the model, because the water column can also contain non-diatom phytoplankton such as dinoflagellates and flagellates (Moran et al. 2012). To test the use of these different FA markers as indicators of i-POM and p-POM, we ran four models using combinations of the FA markers: (a) 16:1n-7, 20:5n-3, and 22:6n-3, (b) 16:1n-7 and 20:5n-3, (c) 20:5n-3 and 22:6n-3, and (d) 20:5n-3. Results are presented as means and 95% credibility intervals (Bayesian confidence interval).

Results

Fatty acid profiles

FA profiles differed among zooplankton species (3-factor PERMANOVA with pairwise comparison *P=0.001*; Fig. 2.2). The FA profiles of *T. libellula* and *C. marshallae/glacialis* were 23% dissimilar with 16:1n-7, 20:1n-11, 20:1n-9, 18:1n-9, and 22:1n-11 contributing to 26% of the dissimilarity (SIMPER). The FA 20:1n-11, 20:1n-9, 22:1n-11, 16:1n-7, and 22:6n-3 (comprised of 29% of dissimilarity) were important in differentiating between *T. libellula* and *T. raschii* (SIMPER). Overall, the proportions of 20:1n-11, 20:1n-9, 22:1n-11, and 22:6n-3 were higher in *T. libellula* compared with *T. raschii* (Kruskal-Wallis ANOVA *P<0.02*; Fig. 2.3). *Calanus marshallae/glacialis* and *T. raschii* were most dissimilar (29%) with 20:1n-9 and 22:1n-11 contributing the greatest differences (SIMPER). Additionally, the proportions of 18:1n-7 were higher in *T. raschii* than in *C. marshallae/glacialis* (Kruskal-Wallis

ANOVA *P<0.002*), while the levels of 16:1n-7 and the longer chain MUFA 20:1n-9, 22:1n-11, and 24:1 were higher in *C. marshallae/glacialis* compared with levels found in *T. raschii* (Kruskal-Wallis ANOVA *P<0.01*). *Calanus marshallae/glacialis* contained the highest amount of total MUFA (38 to 52%, Table 2.3; Kruskal-Wallis ANOVA *P<0.02*). Additionally, the *T. raschii* samples from maximum ice extent and ice melt in 2010 contained the highest amount of PUFA (52%, Table 2.3).

Within each zooplankton species, we found little inter-annual variation in FA profiles (Fig. 2.2). FA profiles of *T. libellula* differed between years only during ice melt (2-factor PERMANOVA with pairwise comparisons *P=0.01*) with 22:6n-3, 16:0, 20:5n-3, 18:1n-9, and 18:1n-7 contributing to 43% of the total dissimilarity (SIMPER). Similarly, FA profiles of *C. marshallae/glacialis* also differed between years during ice melt (2-factor PERMANOVA with pairwise comparisons *P=0.002*) with 16:1n-7, 18:0, 18:4n-3, 22:6n-3, and 20:1n-9 contributing to 27% of the total dissimilarity (SIMPER). FA profiles of *T. raschii* from all ice conditions were not different between years (*P=0.34*). In contrast, some variation in FA profiles among ice conditions was evident within zooplankton species (Fig. 2.2). In 2009, the FA profiles of *T. libellula* differed only between ice melt and ice-free conditions (PERMANOVA pairwise comparisons *P=0.04*). The FA 22:6n-3, 16:0, 20:5n-3, 18:1n-9, and 18:1n-7 contributed to 43% of the total difference (SIMPER). Similarly, the FA profiles of *C. marshallae/glacialis* in 2009 were different between ice melt and ice-free conditions in 2009 (PERMANOVA pairwise comparisons *P=0.04*). The FA 16:0, 22:6n-3, 20:5n-3, 16:1n-7, and 20:1n-9 contributed 38% of the total dissimilarity (SIMPER). In 2010, *C. marshallae/glacialis* FA profiles from ice melt conditions were different from both maximum ice extent and ice-free conditions (2-factor PERMANOVA with pairwise comparison *P<0.04*). The FA 16:1n-7, 18:0, 18:1n-9, 20:5n-3, and 22:1n-11 comprised 32% of the difference between ice melt and maximum ice extent, while 16:1n-5, 18:0, 20:5n-3, 22:6n-3, and 18:1n-9 contributed to 23% of the dissimilarity between ice melt and ice-free conditions (SIMPER). With years combined, *T. raschii* FA profiles were different between maximum ice extent and ice-free conditions (PERMANOVA pairwise comparison *P<0.02*), and 16:1n-7, 22:6n-3, 14:0, 20:4n-6, and 22:5n-3 contributed to 37% of the dissimilarity (SIMPER).

Fatty acid biomarkers

With years and ice conditions combined, some of the FA biomarkers differed among species. For example, the *Calanus* marker (sum of C20 and C22 MUFA) and the carnivory marker (18:1n-9/18:1n-7) were significantly lower

in *T. raschii* compared with the other two species (Kruskal-Wallis ANOVA *P<0.005*; Table 2.3). The diatom/flagellate marker 20:5n-3/22:6n-3 was higher in *T. raschii* than the other two species (Kruskal-Wallis ANOVA *P<0.001*; Table 2.3). In contrast, the diatom/flagellate marker ratios 16:1/16:0 and ΣC16/ΣC18 were higher in *C. marshallae/glacialis* compared with *T. libellula* and *T. raschii* (Kruskal-Wallis ANOVA P<0.01; Table 2.3). These biomarkers reveal different but overlapping levels of omnivory as described by the carnivory and diatom/flagellate marker ratios (18:1n-9/18:1n-7 and 16:1/16:0). This indicates the highest relative level of carnivory in *T. libellula* and the lowest in *T. raschii*, while *C. marshallae/glacialis* had the highest diatom contribution among the three species (Fig. 2.4). The bacterial marker (sum of 15:0, 17:0, and the iso- and anteiso FA i-14:0, i-15:0, ai-15:0, i-16:0, i-17:0, and ai-17:0) in all zooplankton was less than 2.5% (Table 2.3).

For *C. marshallae/glacialis*, both of the diatom/flagellate marker ratios (16:1/16:0 and ΣC16/ΣC18) exceeded a value of 1 (which indicates higher amounts of diatom markers relative to flagellate markers) except for 2009 ice melt and 2010 maximum ice extent (Table 2.3). In contrast, for both *T. libellula* and *T. raschii* only ΣC16/ΣC18 was greater than 1 (except for 2010 maximum ice extent), and 16:1/16:0 was less than 1 (Table 2.3). The diatom to flagellate marker (20:5n-3/22:6n-3) did not show any differences between years and among ice conditions for all zooplankton (Kruskal-Wallis ANOVA *P>0.07*). The carnivory marker ratio PUFA/SFA differed only in *C. marshallae/glacialis* between maximum ice extent and ice melt conditions in 2010 (Kruskal-Wallis ANOVA *P=0.04*).

Carbon stable isotopes of fatty acids

Differences in the $\delta^{13}C_{FA}$ values among species were observed, but there were little annual or seasonal differences within each species. The $\delta^{13}C_{FA}$ values from *C. marshallae/glacialis* were higher than those from both *T. libellula* and *T. raschii* (3-factor PERMANOVA with pairwise comparisons, *P<0.04*). $\delta^{13}C_{FA}$ values were not different between *T. libellula* and *T. raschii* (*P=0.26*). For both *T. libellula* and *T. raschii*, the $\delta^{13}C_{FA}$ values did not differ between years or between ice conditions (2-factor PERMANOVA *P>0.12*). Similarly, the $\delta^{13}C_{FA}$ values of *C. marshallae/glacialis* did not differ between years within ice conditions (i.e., maximum ice extent in 2009 and 2010) or between ice conditions in 2009 (2-factor PERMANOVA with pairwise comparisons, *P>0.10*). In 2010, the $\delta^{13}C_{FA}$ values of *C. marshallae/glacialis* differed only between maximum ice extent and ice melt conditions (2-factor PERMANOVA with pairwise comparisons, *P>0.04*).

In 2009, i-POM $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 were significantly higher than those from p-POM during ice melt conditions (Mann-Whitney U Test, *P<0.04*, Table 2.2). i-POM collected in 2010 during maximum ice conditions also had significantly higher $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 than p-POM. p-POM $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 did not vary between ice conditions (Wang et al. 2014, Table 2.2). The $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 from *T. libellula*, *C marshallae/glacialis*, and *T. raschii* fall within the range of values between i-POM and p-POM (Fig. 2.5). The results from four $\delta^{13}C_{FA}$ mixing models gave varying estimates of the proportional contribution of i-POM to each of the zooplankton species' diet. The estimated amount of FA from i-POM (from models without concentration dependencies) for *T. libellula* ranged between 36% (16% - 56%) (mean, 95% credibility interval) to 72% (50% - 95%), for *C. marshallae/glacialis* between 27% (8% - 47%) to 63% (36% - 96%), and for *T. raschii* the estimates ranged between 39% (0% - 78%) to 71% (47% - 99%) (Table 2.5). Estimates from models without concentration dependencies were similar to concentration dependent models (Table 2.5).

Discussion

Fatty acid biomarkers

FA biomarkers confirmed previously described diets for *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii*. Overall, the proportion of diatoms to flagellates was lowest in *T. libellula* and highest in *T. raschii* indicating that they are primarily herbivorous and that *T. raschii* consumed more diatoms than the other two species. The range in the carnivory marker PUFA/SFA found in *T. libellula* (1.4 – 2.3) falls within the range reported for omnivorous and carnivorous zooplankton (Cripps & Atkinson 2000). Furthermore, another carnivory biomarker ratio (FA 18:1n-9/18:1n-7) from *T. libellula* was similar to ratios reported by Auel et al. (2002) for *T. libellula* and *T. abyssorum* in the European Arctic. The diets of *T. libellula* are mainly comprised of *Calanus* copepodites and may include other zooplankton such as other copepod species, euphausiids, amphipods, mysids, and chaetognaths (Marion et al. 2008, Noyon et al. 2009). The diatom and dinoflagellate FA markers we document, however, also indicate an omnivorous diet in *T. libellula* (Scott et al. 1999). Early juvenile *T. libellula* are known to feed on both phytoplankton and small zooplankton (Søreide et al. 2006, Tamelander et al. 2006, Noyon et al. 2009, 2012) and overwintering individuals may feed on deposited particles on the seafloor (Auel et al. 2002). The low levels of the carnivory marker PUFA/SFA in *C. marshallae/glacialis* (0.7 and 1.8) indicated mostly a herbivorous

and possibly omnivorous feeding strategy (Cripps & Atkinson 2000), which also is consistent with findings from previous studies (Smith 1990, Hobson et al. 2002, Sato et al. 2002, Baier & Napp 2003, Stevens et al. 2004b). As indicated by the carnivory biomarker FA 18:1n-9/18:1n-7, *T. libellula* and *C. marshallae/glacialis* were more carnivorous than *T. raschii*. This is further supported by the stronger presence of the *Calanus* copepod marker (sum of C20 and C22 monounsaturated FA) in *T. libellula* than in *T. raschii*, although the existence of C20 and C22 MUFA in *T. raschii* suggests that they were ingesting some *Calanus* copepodites or eggs. The ratios for PUFA/SFA as a carnivory marker in *T. raschii* ranged widely (0.6 and 2.4) and are consistent with the ratios found in Antarctic herbivorous zooplankton (0.7 – 1.4), but also overlap with the lower ranges found in Antarctic omnivorous (range 0.9 – 3.8) and predatory zooplankton (range 1.5 – 5.2) (Cripps & Atkinson 2000). This suggests a certain degree of omnivory in *T. raschii* in this study. This finding also is consistent with reports that *T. raschii* is primarily herbivorous, but can be carnivorous and may switch to detrital feeding during the winter (Mauchline & Fischer 1969, Falk-Petersen et al. 1981, Sargent & Falk-Petersen 1981, Smith 1991, Hagen & Auel 2001, Hop et al. 2006). The proportion (% total FA) of bacterial FA markers (sum of 15:0, 17:0, and the iso- and anteiso FAs) in all three species were low and comparable to those found by Søreide et al. (2013) for several zooplankton species, including *T. libellula*, in the European Arctic. Therefore, bacteria did not substantially contribute to zooplankton diets in this study.

Fatty acid profiles

FA profiles showed that diets differed between *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii*, which corroborates with previous studies. The variability in FA profiles within each of the zooplankton species was much less than the variability among species. The FA profiles indicated that there was very little variation between 2009 and 2010 in the foraging patterns of all three species, which suggests a similar food base between the two years. Samples from this study were collected during a 'cold' period in the Bering Sea when there was extensive sea ice, cold water temperatures, spring ice-edge blooms, and low inter-annual variability in spring sea ice conditions (Stabeno et al. 2012). Furthermore, a qualitative assessment of phytoplankton communities in the Bering Sea revealed similar diatom species present in spring and summer during 2008 – 2010 (Sherr et al. 2013). Sampling during the spring (maximum ice extent) and summer (ice-free conditions) cruises occurred during the same time in 2009 and 2010. However, sampling during 'ice melt' conditions was later in the season in 2010 than in

2009. There was little ice remaining in 2010 during what is referred to as the 'ice melt' period, and the diatom communities were dominated by planktonic instead of sympagic species (Sherr et al. 2013). Some of the variability in FA profiles of *T. libellula* and *C. marshallae/glacialis* between years during ice melt conditions is likely attributed to the differences in diatom communities during the time of sampling between years.

Although there was little inter-annual variation in the diets of all three species, FA profiles indicated that there was some seasonal variability in their diets. This seasonal change in diet may reflect the seasonal changes in phytoplankton composition on the Bering Sea shelf where algal biomass in the spring is dominated by sea ice and planktonic diatoms (Sukhanova et al. 1999, Lomas et al. 2012, Moran et al. 2012) and can be succeeded in the summer by non-diatom phytoplankton such as dinoflagellates, cryoptophytes, *Phaeocystis* spp., and *Synechococcos* spp. (Moran et al. 2012). Sporadic blooms of the diatoms *Chaetoceros* spp. and *Thalassiosira* spp. also occur in the summer in the eastern Bering Sea (Sukhanova et al. 1999, Sambrotto et al. 2008). Analysis of FA profiles from p-POM samples indicated a seasonal change in algal taxa in the water column in 2010, with an increase in diatoms as the ice melted in the spring followed by a decrease in the diatom signal as the ice disappeared (Wang et al. 2014). The diatom/flagellate FA biomarker 20:5n-3/22:6n-3 in *T. raschii* was twice as high as that in the other two species, implying that *T. raschii* selectively fed on diatoms in the Bering Sea. *Calanus glacialis* may also exhibit preferential or exclusive feeding on diatoms (Graeve et al. 1994, Søreide et al. 2008), and this feeding strategy may propagate the algal FA signal through the food chain.

In addition to differences in FA profiles among species, suggesting differences in diets, we found differences in FA profiles within species across seasons that suggest dietary changes. This might be because dietary preferences are known to change with different age classes in zooplankton. For instance, early juvenile *T. libellula* feed on both phytoplankton and small zooplankton (Søreide et al. 2006, Tamelander et al. 2006, Noyon et al. 2009), and older stages feed extensively on *Calanus* copepods (e.g., Scott et al. 1999, Auel et al. 2002, Dalpadado et al. 2008). In Antarctic krill (*Euphausia superba*) changes in FA profiles may be a reflection of differences due to sexual maturity (Cripps et al. 1999). The age structure of *Calanus marshallae/glacialis* populations in the Bering Sea was different between seasons in 2009, with adult females dominating during ice melt and copepodites being dominant during ice-free conditions (Pinchuk & Coyle 2012). This could contribute to the observed differences in *C. marshallae/glacialis* FA profiles between ice melt and ice-free conditions in 2009. In 2010, the populations during ice melt and ice-free conditions along the middle shelf of the Bering Sea were both dominated by copepodites

(Pinchuk & Coyle 2012) and accordingly, there was no seasonal difference between FA profiles in our samples. Variability in FA profiles could also stem from spatial variability. In 2009 and 2010 during ice-free conditions, younger copepodite stages occurred in the north, while older stages dominated in the south along the 70-m isobath in the middle shelf of the Bering Sea (Pinchuk & Coyle 2012). *Calanus marshallae/glacialis* samples in this study were collected mostly on the northern part of the middle shelf and south of St. Lawrence Island, and the effect of sampling location on variability of FA profiles is unknown. Samples were collected widely across the Bering Sea shelf; however, not enough samples were collected at each station to examine the effect of spatial variability.

Carbon stable isotopes of fatty acids

Despite variability in diets inferred from FA profiles and biomarkers, the $\delta^{13}C_{FA}$ data indicate that all three zooplankton species incorporated sympagic sources of FA between March and July in 2009 and 2010. Our results are comparable to those found by Søreide et al. (2006, 2008, 2013), where the contribution of sympagic carbon to zooplankton was estimated to be as high as 50% and up to 70% in *Calanus* copepods in the European Arctic. Our estimated range of the proportional contribution of i-POM to zooplankton in the Bering Sea (27% – 71%) is also within the range of estimates of sea ice algal contribution to *T. raschii* from the Chukchi region off of Barrow, Alaska (20% – 74%; Budge et al. 2008). Some of the variability in our model estimates could come from the different FA used. The FA 20:5n-3 originates mainly from diatoms and 22:6n-3 predominately comes from flagellates (Sargent et al. 1987, Volkman et al. 1989, Dunstan et al. 1994, Graeve et al. 1994, Reuss & Poulsen 2002). In the Bering Sea, algal biomass in the spring is dominated by sea ice and planktonic diatoms (Sukhanova et al. 1999, Lomas et al. 2012, Moran et al. 2012), and blooms of the diatoms *Chaetoceros* spp. and *Thalassiosira* spp. also occur in the summer in the eastern Bering Sea (Sukhanova et al. 1999, Sambrotto et al. 2008). In addition to elevated proportions of the FA 20:5n-3, feeding on diatoms by herbivorous consumers can be detected using FA 16:1n-7 (Graeve et al. 1994, Dalsgaard et al. 2003). Nevertheless, 16:1n-7 in consumers can also result from *de novo* synthesis and chain shortening of other FA and might not be appropriate for estimating diatom sources in omnivorous and carnivorous animals. Therefore, the model using only the diatom FA marker 20:5n-3 may be the most accurate to estimate the proportional contribution of i-POM if diatoms dominated the POM communities. In fact, 90% of the algal species identified in sea ice cores and water samples collected during between 16 March and 2 May 2009 (maximum ice extent and ice melt periods) in the Bering Sea were diatoms, and there was no significant

difference between algal species identified in sea ice and water samples (A. Syzmanski unpublished data). However, the use of the flagellate marker 22:6n-3 should be taken into consideration for the ice melt period when non-diatom phytoplankton may contribute substantially to the algal composition of POM, as using only the diatom FA markers in the modeling may underestimate the proportional contribution of non-diatom POM.

The method of analyzing $\delta^{13}C_{FA}$ of specific FA relies on the assumptions that these FA cannot be synthesized or modified by the species in question, and that the isotopic fractionation associated with the metabolism of FA analyzed is negligible (Budge et al. 2008, 2011). Fractionation of FAs from POM to zooplankton, depending on the direction of enrichment, would influence the estimates of the model. For example, if the $\delta^{13}C_{FA}$ became heavier in the consumer relative to the source, estimates would be biased toward the heavier source (in this case i-POM). In marine environments where long-chain essential PUFA such as 20:5n-3 and 22:6n-3 are abundant, there is strong evidence in fish that the activity level of enzymes responsible for FA elongation and desaturation is minor (Tocher 2003). Feeding experiments with herbivorous copepod species have shown that phytoplankton-derived FA such as 16:1n-7, 20:5n-3, and 22:6n-3 are incorporated largely unchanged (reviewed by Dalsgaard et al. 2003). Thus, if these FAs are incorporated into zooplankton without modification, it is reasonable to assume that their stable isotopic compositions are also unmodified. Additionally, Parrish et al. (2012) showed that there was little modification or sequestration of the PUFA 20:5n-3 and 22:6n-3 by *Calanus* copepods, and Budge et al. (2011) found no isotopic discrimination of these FA between the diet and adipose tissue of two species of eiders (*Polysticta stelleri* and *Somateria fischeri*). Although 16:1n-7 can be used as a diatom marker, it can also result from biosynthesis in animals (e.g., Rangan & Smith 2002). If this were the case, 16:1n-7 that was biosynthesized would be more depleted in ^{13}C relative to dietary 16:1n-7 because lipids in animal tissues have lower $\delta^{13}C$ values than that of their diets due to 13C discrimination during lipid synthesis (DeNiro & Epstein 1977). Therefore, if a FA within an animal were coming from biosynthesis, it would have a lower $\delta^{13}C_{FA}$ value than for other FA that came strictly from the diet, and thus lower the contribution estimates of i-POM in the consumer. The models that include 16:1n-7 did not result in consistently lower estimates of i-POM, which provides evidence that 16:1n-7 might in fact be derived from the diet and is not biosynthesized; therefore, other processes besides or in addition to *de novo* synthesis could be contributing to the variability in estimates. We acknowledge that future controlled feeding experiments of zooplankton species with different foraging strategies (i.e., herbivory, omnivory, carnivory) would be valuable to

further examine the effect of dietary modification on $\delta^{13}C_{FA}$ values and isotopic fractionation of FA. Despite these unknowns, all the zooplankton $\delta^{13}C_{FA}$ values fall within the i-POM and p-POM values.

Mixing models often assume that the proportional contribution of a diet source to a consumer is the same for all components included, in this case FAs (Phillips & Koch 2002). However, the proportions of FAs can vary among diet sources, thus the estimates of the proportional contribution of sources could be biased toward one source or another, depending on their relative proportions. The proportions of the FAs used in the models (16:1n-7, 20:5n-3, and 22:6n-3) only differed between i-POM and p-POM in 2009 by between 1.5% and 3%. In contrast, the proportions of these FAs in i-POM compared with p-POM in 2010 were much greater, especially for the diatom markers 16:1n-7 and 20:5n-3. For example, the percentage of 16:1n-7 in p-POM from ice-melt in 2010 (28%) was over twice as much as the percentage in i-POM during maximum ice extent in 2010 (12%). Despite these differences in the relative proportions of FAs used in the model between POM sources, the concentration dependent model estimates were very similar to the results from the models that assumed that the proportions of FAs were the same between POM sources.

Our estimates of sea ice-derived FA to zooplankton did not completely support our hypothesis that the predominately herbivorous *C. marshallae/glacialis* and *T. raschii* would have the highest contributions of sea ice-derived FA during maximum ice extent, and that it would decrease as the ice melted and progressed into ice-free conditions. The average contribution of i-POM estimated by all models was similar between the two species during maximum ice extent in both years, but suggests that *T. raschii* consumed more sea ice-derived FA than *Calanus* spp. did during ice melt and ice-free conditions in both years. For both species, the average estimates of i-POM contribution during ice-free conditions decreased from ice melt conditions in 2009 as predicted, but increased in 2010. The contrast in seasonal patterns could be due to a larger pelagic summer diatom bloom in 2009 than in 2010. In fact, the average chlorophyll *a* concentration across all stations during the summer cruise in 2009 (1.03 ± 0.86 µg L-1) was significantly higher than the average during the summer cruise in 2010 (0.70 ± 0.85 µg L-1; Student's t-test, *P=0.001*). However, this does not necessarily confirm that pelagic primary production was higher in 2009 than in 2010 because different stations were sampled between both years.

The average contribution of sea ice algal FA estimated by all models was lower in *T. libellula* than the other two species only during ice melt in 2009, but was still substantial at 46%. Interestingly, the average estimate for *T. libellula* was ~10% higher than both predominantly herbivorous species during ice-free conditions in 2009,

and *C. marshallae/glacialis* during ice melt and ice-free conditions in 2010. Estimates for *T. libellula* also increased in 2009 from maximum ice extent to ice melt conditions, and from ice melt to ice-free conditions in 2010. These patterns observed in *T. libellula* may be explained by a seasonal increase in abundance of its prey, *C. marshallae/glacialis*. *Calanus marshallae/glacialis* populations in the Bering Sea increased after a shift to cold years in 2006 with heavy spring sea ice cover compared to the warmer years of 2001 – 2005 (Baier & Napp 2003, Coyle et al. 2011), and also increased seasonally along the middle shelf in 2009 and 2010 (Pinchuk & Coyle 2012). The greater abundance of *C. glacialis*, a seasonal increase in *C. marshallae/glacialis* populations could increase the i-POM contribution in consumers such as *T. libellula* that prey on them.

The variation in the estimated proportional contribution of i-POM FA to zooplankton could also be due to a delay in carbon stable isotope or lipid turnover in zooplankton. Although dietary lipids are incorporated in copepods in as little as 24 h, only 40% of the lipids had turned over after 14 days in feeding experiments with *C. glacialis* females (Graeve et al. 2005). For the Arctic gammarid amphipod *Onisimus litoralis*, sufficient changes in carbon stable isotopes in tissues can be detected in animals collected in the spring under ice-cover and animals collected four weeks later, whereas during ice-free conditions animals may integrate carbon from their diet over a period of months (Kaufman et al. 2008). Therefore, the estimates of i-POM contribution for samples we collected during ice-free conditions could reflect FA sources from maximum ice extent and ice-melt conditions because of slower turnover of carbon of animals during ice-free conditions. For example, the average estimates from all models were higher during ice-free conditions in both years for *T. libellula*, and in 2010 for both predominant herbivores, *Calanus* spp. and *T. raschii*. In 2009, samples collected during ice-melt and ice-free conditions were collected approximately four and 15 weeks after samples that were collected during maximum ice conditions. In 2010, samples collected during ice-melt and ice-free conditions were collected approximately 11 and 16 weeks, respectively, after samples were collected during maximum ice conditions. The possibility of slower turnover of carbon isotopes between seasons complicates the interpretation of our estimates, suggesting that model results during ice-melt and ice-free conditions could reflect the proportional contribution of i-POM earlier during periods of ice cover. In addition to timing of sample collection, the variability in the amount of ice cover and timing of break up between years may also affect the variability in i-POM contribution to zooplankton between years. In fact, the number of days with ice cover after 15 March in the vicinity of Mooring 2 on the Bering Sea shelf was 46 d in 2009

and 38 d in 2010, and the ice cover index (relative to the 1981 – 2000 mean) was 3.54 in 2009 and 3.28 in 2010 (NOAA 2013).

Regardless of which FA were used, the different mixing models provided similar estimates and showed that *T. libellula*, *C. marshallae/glacialis*, and *T. raschii* in the Bering Sea in 2009 and 2010 consumed substantial (27% – 71%) amounts of sea ice-derived FA and were possibly still consuming it as the ice retreated. The estimated proportional contributions of i-POM FA to zooplankton in this study are representative of heavy ice conditions in the Bering Sea as they occurred in 2009 and 2010 and may be used as a baseline for comparison with future studies conducted during warmer years with less sea ice cover. Predicted changes in timing of sea ice retreat could be detrimental to zooplankton species that are dependent on the spring bloom. For example in the Bering Sea, *C. glacialis* grazes on ice algae before ice melt and pelagic reproduction events that are triggered by the release of ice algae into the water column (e.g., Durbin & Casas 2014). *T. raschii* fuel spring and summer reproduction from the spring bloom (Harvey et al. 2012). Consequently, a mismatch between the timing of the spring bloom and reproduction and feeding could be unfavorable to these species and others that depend on them for food. In addition to changes in the timing of sea ice retreat, the predicted loss of sea ice and subsequent decrease in sympagic primary productivity will lead to a reduction in available sea ice-derived FAs to zooplankton and possibly alter the overall food web dynamics of the Bering Sea. Current sea ice loss has driven a 30% increase in net primary productivity in the Chirkov Basin and a 20% increase in the Arctic Ocean (Brown & Arrigo 2012). Future loss of sea ice is also predicted to increase net primary production on the Bering Sea shelf (Brown & Arrigo 2012). Thus, the estimated contribution of p-POM to *T. libellula*, *C. marshallae/glacialis*, and *T. raschii* cannot be ignored (29 – 73%) and implies that these three species also use pelagic production. As such, our results suggest that these zooplankton species in the Bering Sea are linked, but not exclusively, to the sea ice algal community as a source of FAs. Thus, depending on the timing of pelagic production relative to ice algal production and trophodynamic phasing, these zooplankton species may be resilient to climate-induced changes at the base of the food web.

Acknowledgments

This project was funded by the National Science Foundation (ARC-0902177 and 0732767). Financial support for S.Wang was also provided by the NSF, North Pacific Research Board Graduate Research Award, the University of Alaska Center for Global Change Student Research Grant with funds from the Cooperative Institute for Alaska Research, Robert Byrd Award, Dieter Family Marine Science Research Scholarship, and the Ken Turner Memorial Fellowship. Ice retreat and ice cover index data were obtained from http://www.beringclimate.noaa.gov/data/ a website maintained by the Pacific Marine Environmental Laboratory (PMEL). Chlorophyll a data provided by NCAR/EOL under sponsorship of the National Science Foundation. http://data.eol.ucar.edu/. We thank J. Weems and S. Brennan for assisting with sample collections and A. Timmins (Dalhousie), T. Howe (UAF), N. Haubenstock (UAF), C. Graham (UAF), and C. Stark (UAF) for laboratory assistance. We are grateful for the excellent assistance of the crew and captains of the USCGC Polar Sea and Healy and the UNOLS vessel Thomas G. Thompson, and chief scientists L. Cooper (University of Maryland Center for Environmental Science, HLY0901 and PSEA10-01), C. Ashjian (Woods Hole Oceanographic Institution, HLY0902 and TN249), R. Sambrotto (Lamont-Doherty Earth Observatory, KN195-10), and D. Shull (Western Washington University, TN250). Finally, we thank L. Oxtoby and L. Horstmann-Dehn for helpful discussions and constructive comments that improved the manuscript. Author Contributions: SWW wrote the manuscript. SWW performed the compound-specific stable isotope analysis and analyzed the data. MJW and SMB formulated the concept. SMB developed methodology and performed the fatty acid laboratory analysis. RRG and KI conducted fieldwork and provided editorial advice. AMS provided editorial advice.

References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Aust Ecol 26:32-46

Arrigo KR, Mock T, Lizotte MP (2010) Primary producers and sea ice. In: Thomas DN, Dieckmann GS (eds) Sea Ice. Wiley-Blackwell, Oxford, United Kingdom, p 283-325

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383

Baier CT, Napp JM (2003) Climate-induced variability in *Calanus marshallae* populations. J Plankton Res 25:771-782

Bluhm BA, Gradinger R (2008) Regional variability in food availability for arctic marine mammals. Ecol Appl 18:S77-S96

Brown ZW, Arrigo KR (2012) Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES J Mar Sci 69:1180-1193

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mammal Sci 22:759-801

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29:1547-1559

Budge SM, Wang SW, Hollmén TE, Wooller MJ (2011) Carbon isotopic fractionation in eider adipose tissue varies with fatty acid structure: implications for trophic studies. J Exp Biol 214:3790-3800

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117-129

Ciannelli L, Brodeur RD, Napp JM (2004) Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea. Mar Biol 144:515-526

Claustre H, Marty J-C, Cassiani L, Dagaut J (1988/1989) Fatty acid dynamics in phytoplankton and microzooplankton communities during a spring bloom in the coastal Ligurian Sea: ecological implications. Mar Microb Food Webs 3:51-66

Conover RJ, Huntley M (1991) Copepods in ice-covered seas—Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J Mar Syst 2:1-41

Coyle KO, Eisner LB, Mueter FJ, Pinchuk AI, Janout MA, Cieciel KD, Farley EV, Andrews AG (2011) Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fish Oceanogr 20:139-156

Cripps GC, Atkinson A (2000) Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. Can J Fish Aquatic Sci 57:31-37

Cripps GC, Watkins JL, Hill HJ, Atkinson A (1999) Fatty acid content of Antarctic krill *Euphausia superba* at South Georgia related to regional populations and variations in diet. Mar Ecol Prog Ser 181:177-188

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep Sea Res II 55:2266-2274

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225-340

DeNiro M, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197:261-263

Dunstan GA, Volkman JK, Barrett SM, Leroi JM (1994) Essential polyunsaturated fatty acids from 14 species of diatom (*Bacillariophyceae*). Phytochem 35:155-155

Durbin EG, Casas MC (2014) Early reproduction by *Calanus glacialis* in the Northern Bering Sea: the role of ice algae as revealed by molecular analysis. J Plankton Res 36:523-541

Falk-Petersen S, Dahl TM, Scott CL, Sargent JR, Gulliksen Br, Kwasniewski S, Hop H, Millar R-M (2002) Lipid biomarkers and trophic linkages between ctenophores and copepods in Svalbard waters. Mar Ecol Prog Ser 227:187-194

Falk-Petersen S, Gatten RR, Sargent JR, Hopkins CCE (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: seasonal changes in the lipid class composition of *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa raschii* (M. Sars), and *T. inermis* (Krøyer). J Exp Mar Biol Ecol 54:209-224

Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Can J Fish Aquatic Sci 57:178-191

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web; Proceedings of the 24th European Marine Biology Symposium. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine enviroment. Aberdeen University Press, Aberdeen, p 315-333

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic Calanus. Mar Biol Res 5:18-39

Falk-Petersen S, Sargent JR, Tande KS (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. Polar Biol 8:115-120

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497-509

Frost KJ, Lowry LF (1981) Foods and trophic relationships of cetaceans in the Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle, p 825-836

Gradinger RR (2002) Sea ice microorganisms. In: Bitten G (ed) Encyclopedia of environmental microbiology. Wiley and Sons, Hoboken, New Jersey, USA, p 2833-2844

Graham C, Oxtoby L, Wang SW, Budge SM, Wooller MJ (2014) Sourcing fatty acids to juvenile polar cod (*Boreogadus saida*) in the Beaufort Sea using compound-specific stable carbon isotope analyses. Polar Biol doi: 10.1007/s00300-014-1470-5

Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on feeding experiments with a ^{13}C labelled diatom. J Exp Mar Biol Ecol 317:109-125

Graeve M, Kattner G, Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: Experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97-110

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53-61

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annual Rev Mar Sci 4:63-78

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313-326

Harvey HR, Pleuthner RL, Lessard EJ, Bernhardt MJ, Shaw CT (2012) Physical and biochemical properties of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Thysanoessa longipes* in the eastern Bering Sea. Deep Sea Res II 65-70:173-183

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Res II 49:5131-5150

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Progr Oceanogr 71:182-231

Horner RA (1985) Taxonomy of sea ice microalgae. In: Horner RA (ed) Sea Ice Biota. CRC Press, Boca Raton, Florida, USA, p 147-158

Hunt GL, Jr., Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Res II 49:5821-5853

Kattner G, Hagen W (1995) Polar herbivorous copepods – different pathways in lipid biosynthesis. ICES J Mar Sci 52:329-335

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158:11-22

Kürten B, Frutos I, Struck U, Painting SJ, Polunin NVC, Middelburg JJ (2013) Trophodynamics and functional feeding groups of North Sea fauna: a combined stable isotope and fatty acid approach. Biogeochem 113:189-212

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306

Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Progr Oceanogr 90:18-32

Lomas MW, Moran SB, Casey JR, Bell DW, Tiahlo M, Whitefield J, Kelly RP, Mathis JT, Cokelet ED (2012) Spatial and seasonal variability of primary production on the Eastern Bering Sea shelf. Deep Sea Res II 65–70:126-140

Marion A, Harvey M, Chabot D, Brethes J (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. Mar Ecol Prog Ser 373:53-70

Mauchline J, Fischer LR (1969) The Biology of Euphausiids, Vol 7. Academic Press, London and New York

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290-297

Michel C, Legendre L, Ingram RG, Gosselin M, Levasseur M (1996) Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers. J Geophys Res 101:18345-18360

Moran SB, Lomas MW, Kelly RP, Gradinger R, Iken K, Mathis JT (2012) Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea. Deep Sea Res II 65–70:84-97

Nelson M, Phleger C, Mooney B, Nichols P (2000) Lipids of gelatinous antarctic zooplankton: Cnidaria and Ctenophora. Lipids 35:551-559

Nelson RJ, Carmack EC, McLaughlin FA, Cooper GA (2009) Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. Mar Ecol Prog Ser 381:129-138

NOAA (2013) Bering climate: A current view of the Bering Sea ecosystem and climate. http://www.beringclimate.noaa.gov (accessed 10 Dec 2013)

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32:1559-1570

Noyon M, Narcy F, Gasparini S, Mayzaud P (2012) Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). Mar Biol 159:805-816

NSIDC (2009) National Snow and Ice Data Center. Arctic Sea Ice Younger, Thinner as Melt Season Begins. http://nsidcorg/arcticseaicenews/2009/04/arctic-sea-ice-younger-thinner-as-melt-season-begins/

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672

Parrish CC (1999) Determination of total lipid, lipid classes and fatty acids in aquatic samples. In: Arts MT, Wainman BC (eds) Lipids in Freshwater Ecosystems. Springer-Verlag, New York, p 4-12

Parrish CC, French VM, Whiticar MJ (2012) Lipid class and fatty acid composition of copepods (*Calanus finmarchicus*, *C. glacialis*, *Pseudocalanus* sp., *Tisbe furcata* and *Nitokra lacustris*) fed various combinations of autotrophic and heterotrophic protists. J Plankton Res 34:356-375

Phillips DL, Koch PL (2002) Incorporating concentration dependence in stable isotope mixing models. Oecologia 130:114-125

Pinchuk AI, Coyle KO (2012) Variability in *Calanus* spp. populations on the eastern Bering Sea shelf during the recent cold phase. Abstract 12228, Ocean Sciences Meeting, Salt Lake City, Utah, USA, February 20-24, 2012

Pinchuk AI, Coyle KO, Farley EV, Renner HM (2013) Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiidae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web. ICES J Mar Sci 70:1244-1254

Rangan VS, Smith S (2002) Fatty acid synthesis in eukaryotes. In: Vance DE, Vance JE (eds) Lipid biochemistry: an introduction, 4th ed. Blackwell Science, Oxford, United Kingdom, p 151-179

Reuss N, Poulsen L (2002) Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar Biol 141:423-434

Richter-Menge J, Overland J (2010) Arctic Report Card 2010. http://www.arctic.noaa.gov/reportcard

Sambrotto RN, Mordy C, Zeeman SI, Stabeno PJ, Macklin SA (2008) Physical forcing and nutrient conditions associated with patterns of Chl *a* and phytoplankton productivity in the southeastern Bering Sea during summer. Deep Sea Res II 55:1745-1760

Sargent JR, Falk-Petersen S (1981) Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: Lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid-winter. Mar Biol 62:131-137

Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. Hydrobiologia 167-168:101-114

Sargent JR, Parkes RJ, Mueller-Harvey I, Henderson RJ (1987) Lipid biomarkers in marine ecology. In: Sleigh MA (ed) Microbes in the Sea. Wiley and Sons, New York, p 119-138

Sato M, Sasaki H, Fukuchi M (2002) Stable isotopic compositions of overwintering copepods in the arctic and subarctic waters and implications to the feeding history. J Mar Systems 38:165-174

Scott CL, Falk-Petersen S, Gulliksen B, Lonne OJ, Sargent JR (2001) Lipid indicators of the diet of the sympagic amphipod *Gammarus wilkitzkii* in the Marginal Ice Zone and in open waters of Svalbard (Arctic). Polar Biol 24:572-576

Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biol 21:65-70

Sherr EB, Sherr BF, Ross C (2013) Microzooplankton grazing impact in the Bering Sea during spring sea ice conditions. Deep Sea Res II 94:57-67

Smith SL (1990) Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. Mar Biol 106:59-69

Smith SL (1991) Growth, development and distribution of the euphausiids *Thysanoessa raschii* (M. Sars) and *Thysanoessa inermis* (Krøyer) in the southeastern Bering Sea. Polar Res 10:461-478

Søreide JE, Carroll ML, Hop H, Ambrose WG, Hegseth EN, Falk-Petersen S (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Mar Biol Res 9:831-850

Søreide JE, Falk-Petersen S, Hegseth EN, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep Sea Res II 55:2225-2244

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Progr Oceanogr 71:59-87

Springer AM, Roseneau DG (1985) Copepod-based food webs: Auklets and oceanography in the Bering Sea. Mar Ecol Prog Ser 21:229-237

Stabeno P, Napp J, Mordy C, Whitledge T (2010) Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: Sea ice, tides and winds. Progr Oceanogr 85:180-196

Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the south-eastern Bering Sea. Fish Oceanogr 10:81-98

Stabeno PJ, Kachel NB, Moore SE, Napp JM, Sigler M, Yamaguchi A, Zerbini AN (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res II 65–70:31-45

Stevens CJ, Deibel D, Parrish CC (2004a) Copepod omnivory in the North Water Polynya (Baffin Bay) during autumn: spatial patterns in lipid composition. Deep Sea Res I 51:1637-1658

Stevens CJ, Deibel D, Parrish CC (2004b) Species-specific differences in lipid composition and omnivory indices in Arctic copepods collected in deep water during autumn (North Water Polynya). Mar Biol 144:905-915

Strasburger WW, Hillgruber N, Pinchuk AI, Mueter FJ (2013) Feeding ecology of age-0 walleye pollock (*Gadus chalcogramma*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea. Deep Sea Res II doi: 10.1016/j.dsr2.2013.10.007

Sukhanova I, Semina H, Venttsel M (1999) Dynamics of the Bering Sea. In: Loughlin T, Ohtani K (eds) Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska, p 453-484

Tamelander T, Renaud PE, Hop H, Carroll ML, Jr. WGA, Hobson KA (2006) Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Mar Ecol Prog Ser 310:33-46

Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. Rev Fish Sci 11:107-184

Tourangeau S, Runge JA (1991) Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. Mar Biol 108:227-233

Viso A-C, Marty J-C (1993) Fatty acids from 28 marine microalgae. Phytochem 34:1521-1533

Volkman JK, Jeffrey SW, Nichols PD, Rogers GI, Garland CD (1989) Fatty acid and lipid composition of 10 species of microalgae used in mariculture. J Exp Mar Biol Ecol 128:219-240

Wang SW, Budge SM, Gradinger RR, Iken K, Wooller MJ (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699-712

Table 2.1. Sample information for i-POM and p-POM collected from the Bering Sea shelf in 2009. Samples were taken on the cruise HLY0902 during ice melt conditions. Details for i-POM and p-POM collected in 2010 are described in Wang et al. (2014).

POM type	Date (m/dd/yyyy)	Station number	Station name	Latitude °N	Longitude °W	No. of samples
i-POM (N=6)	4/14/2009	29	St. 29	61.792	-176.802	2
	4/16/2009	35	SL 9	63.094	-173.291	1
	5/01/2009	45	St. 92	61.589	-173.709	2
	5/02/2009	93	BN1	62.333	-172.703	1
p-POM (N=6)	4/27/2009	73	BL4	60.537	-176.205	2
	4/29/2009	85	BL15	59.55	-175.096	1
	4/30/2009	90	BL20	59.555	-175.150	1
	5/06/2009	115	BL21	59.444	-174.082	1
	5/06/2009	116	BL15/2	59.552	-175.150	1

Table 2.2. $\delta^{13}C_{FA}$ values of 16:1n-7, 20:5n-3, and 22:6n-3 from i-POM and p-POM collected in the Bering Sea in 2009 and 2010 (Wang et al. 2014). N = sample sizes: some are given as ranges, as not all $\delta^{13}C_{FA}$ values could be determined from all samples (Wang et al. 2014). nd = samples not collected. Mean ± 1SD

		i-POM			p-POM		
		Max ice	Ice melt	Ice-free	Max ice	Ice melt	Ice-free
2009	N	0	4-6	0	0	6	0
	16:1n-7	nd	-21.0 ± 6.8	nd	nd	-28.8 ± 1.5	nd
	20:5n-3	nd	-26.5 ± 3.0	nd	nd	-29.7 ± 1.3	nd
	22:6n-3	nd	-26.2 ± 2.9	nd	nd	-30.4 ± 0.8	nd
2010	N	12	0	0	11-12	20	14
	16:1n-7	-25.2 ± 4.5	nd	nd	-28.4 ± 1.2	-29.7 ± 1.7	-29.5 ± 1.6
	20:5n-3	-26.5 ± 2.8	nd	nd	-29.7 ± 1.6	-29.3 ± 1.6	-30.2 ± 1.9
	22:6n-3	-23.8 ± 3.2	nd	nd	-27.0 ± 2.1	-27.3 ± 2.5	-28.3 ± 2.3

Table 2.3. Fatty acid (FA) biomarkers for (a) *Themisto libellula*, (b) *Calanus marshallae/glacialis*, and (c) *Thysanoessa raschii* collected in 2009 and 2010. Samples were collected from the Bering Sea during maximum ice, ice melt, and ice-free periods. The bacteria marker is the sum of 15:0, 17:0, and the iso and anteiso FA (i-14:0, i-15:0, ai-15:0, i-16:0, i-17:0, and ai-17:0). The ratios of 16:1/16:0, ΣC16/ΣC18 FA, and 20:5n-3/22:6n-3 represent diatom to flagellate ratios. The *Calanus* marker is the sum of C20 and C22 monounsaturated FA (MUFA). The ratios of 18:1n-9/18:1n-7 and of polyunsaturated FA (PUFA)/saturated FA (SFA) represent the degree of carnivory (the greater the ratios, the greater the degree of carnivory). SFA, MUFA, PUFA, and means for each biomarker across species are also reported. *T. libellula* samples were not collected during maximum ice extent in 2009. Values are given as mean ± 1SD

(a) *Themisto libellula*	Overall	2009			2010		
	Average	Max ice	Ice melt	Ice-free	Max ice	Ice melt	Ice-free
N	27		5	8	2	4	8
Bacteria	1.1 ± 0.1		1.1 ± 0.2	1.0 ± 0.2	1.1 ± 0.3	0.7 ± 0.3	1.3 ± 0.5
16:1/16:0	0.6 ± 0.4		0.2 ± 0.7	0.7 ± 0.4	0.4 ± 0.1	0.6 ± 0.3	0.6 ± 0.5
ΣC16/ΣC18	1.2 ± 0.4		1.0 ± 0.1	1.4 ± 0.3	0.9 ± 0.1	1.3 ± 0.3	1.2 ± 0.6
20:5n-3/22:6n-3	1.0 ± 0.7		0.7 ± 0.1	1.2 ± 0.7	0.7 ± 0.2	1.8 ± 1.1	0.8 ± 0.4
Calanus	11.0 ± 6.8		13.0 ± 5.6	11.6 ± 7.8	9.8 ± 8.9	9.1 ± 7.1	10.4 ± 7.5
Carnivory	3.1 ± 1.5		3.3 ± 0.7	2.4 ± 0.9	4.5 ± 0.9	2.2 ± 0.3	3.6 ± 2.4
PUFA/SFA	1.7 ± 0.5		1.7 ± 0.5	1.9 ± 0.6	2.3 ± 1.2	1.4 ± 0.2	1.5 ± 0.2
SFA	23.1 ± 4.0		24.0 ± 5.6	21.4 ± 1.4	19.3 ± 2.1	25.0 ± 1.5	24.4 ± 5.2
MUFA	37.3 ± 8.7		36.3 ± 3.3	36.4 ± 9.8	36.7 ± 16.6	40.3 ± 4.7	37.4 ± 11.1
PUFA	38.3 ± 7.9		38.5 ± 4.7	41.0 ± 10.1	42.5 ± 18.4	34.2 ± 4.0	36.6 ± 6.2

(b) *Calanus*	Overall	2009			2010		
marshallae/glacialis	Average	Max ice	Ice melt	Ice-free	Max ice	Ice melt	Ice-free
N	24	4	6	2	4	6	2
Bacteria	1.6 ± 0.7	2.5 ± 0.3	1.7 ± 0.5	1.0 ± 0.0	2.1 ± 0.4	0.9 ± 0.2	1.2 ± 0.5
16:1/16:0	1.5 ± 1.1	1.4 ± 0.6	0.7 ± 0.5	2.4 ± 0.2	0.6 ± 0.3	2.5 ± 1.3	2.4 ± 0.7
ΣC16/ΣC18	2.6 ± 1.2	1.7 ± 0.2	1.8 ± 0.5	3.3 ± 0.1	1.7 ± 0.3	4.1 ± 1.2	3.2 ± 0.7
20:5n-3/22:6n-3	1.1 ± 0.7	0.6 ± 0.1	0.8 ± 0.3	2.6 ± 0.4	0.7 ± 0.4	1.4 ± 0.9	0.8 ± 0.0
Calanus	13.2 ± 5.2	18.1 ± 5.6	13.7 ± 5.4	17.2 ± 1.6	12.2 ± 6.0	10.6 ± 2.8	7.7 ± 2.1
Carnivory	2.3 ± 1.2	3.4 ± 0.9	1.7 ± 0.7	2.6 ± 0.1	2.2 ± 0.4	1.5 ± 0.5	4.6 ± 2.2
PUFA/SFA	1.3 ± 0.5	0.7 ± 0.3	1.2 ± 0.5	1.8 ± 0.2	1.2 ± 0.4	1.8 ± 0.1	1.1 ± 0.8
SFA	24.4 ± 6.0	27.4 ± 5.0	28.1 ± 6.7	18.2 ± 2.0	27.8 ± 2.8	18.7 ± 1.8	24.1 ± 7.2
MUFA	44.1 ± 8.8	50.2 ± 7.8	37.5 ± 10.2	48.4 ± 1.2	38.6 ± 7.0	46.2 ± 6.5	51.6 ± 3.2
PUFA	29.8 ± 8.5	19.7 ± 6.2	32.5 ± 8.6	32.5 ± 0.7	31.4 ± 9.1	34.5 ± 4.6	22.6 ± 10.7

(c) *Thysanoessa raschii*	Overall	2009			2010		
	Average	Max ice	Ice melt	Ice-free	Max ice	Ice melt	Ice-free
N	15	2	4	2	1	4	2
Bacteria	0.7 ± 0.4	0.7 ± 0.1	0.6 ± 0.0	0.6 ± 0.2	1.4	0.7 ± 0.6	0.4 ± 0.0
16:1/16:0	0.5 ± 0.3	0.2 ± 0.0	0.3 ± 0.1	0.6 ± 2.0	0.3	0.8 ± 0.3	0.8 ± 0.1
ΣC16/ΣC18	1.6 ± 0.6	1.0 ± 0.0	1.2 ± 0.3	2.0 ± 2.1	0.7	1.9 ± 0.7	2.2 ± 0.2
20:5n-3/22:6n-3	2.4 ± 1.0	1.3 ± 0.1	2.1 ± 0.6	3.2 ± 0.3	1.3	2.4 ± 0.3	4.3 ± 0.1
Calanus	3.0 ± 3.2	2.5 ± 0.7	2.8 ± 0.5	2.3 ± 1.2	4.0	4.4 ± 6.6	1.6 ± 0.0
Carnivory	1.3 ± 0.6	1.2 ± 0.3	1.0 ± 0.3	1.3 ± 0.4	3.2	1.3 ± 0.4	0.7 ± 0.1
PUFA/SFA	1.6 ± 0.7	2.4 ± 0.3	2.3 ± 0.2	0.6 ± 0.1	1.5	1.4 ± 0.2	0.7 ± 0.1
SFA	27.2 ± 6.6	21.2 ± 1.4	22.5 ± 0.9	39.2 ± 3.4	23.8	25.9 ± 1.5	35.1 ± 1.1
MUFA	32.4 ± 6.6	25.9 ± 1.9	25.0 ± 3.2	36.5 ± 2.9	37.4	35.5 ± 2.7	41.1 ± 0.5
PUFA	39.5 ± 12.0	51.8 ± 3.2	51.9 ± 3.1	23.9 ± 0.5	36.5	37.4 ± 2.5	23.4 ± 1.7

Table 2.4 Percentages of 16:1n-7, 20:5n-3, 22:6n-3 in i-POM and p-POM from 2009 and 2010. Values used as concentration dependencies in the SIAR stable isotope mixing models using diatom markers 16:1n-7, 20:5n-3, and flagellate marker 22:6n-3 as sources. Mean ± 1 SD

	16:1n-7		20:5n-3		22:6n-3	
Source	Mean	SD	Mean	SD	Mean	SD
i-POM 2009	18.7	6.1	20.3	7.6	2.2	0.8
p-POM 2009	16.5	6.2	23.2	4.4	3.8	0.5
i-POM 2010	12.7	5.2	19.6	6.6	2.5	0.8
p-POM 2010 Max	5.6	4.0	5.5	5.4	2.5	1.0
p-POM 2010 Melt	28.1	12.5	13.7	5.0	3.7	2.0
p-POM 2010 Free	10.0	6.6	10.2	4.0	9.0	2.6

Table 2.5. Estimates of i-POM (%) in *Themisto libellula, Calanus marshallae/glacialis*, and *Thysanoessa raschii* from four SIAR mixing models (a) without and (b) with concentration dependencies (Table 2.4). Samples were collected from the Bering Sea in 2009 and 2010 during maximum ice, ice melt, and ice-free conditions. *T. libellula* samples were not collected during maximum ice extent in 2009. Samples sizes are shown in Table 1. Mean (95% credibility interval)

	2009 (a)			2009 (b)		
Themisto libellula	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3		46 (25 – 65)	51 (27 – 74)		47 (21 – 72)	51 (22 – 81)
16:1n-7, 20:5n-3		36 (16 – 56)	38 (18 – 58)		36 (15 – 58)	36 (16 – 58)
20:5n-3, 22:6n-3		55 (34 – 78)	72 (50 – 95)		62 (38 – 86)	79 (57 – 99)
20:5n-3		47 (16 – 80)	59 (32 – 90)		49 (17 – 81)	61 (34 – 92)
	2010 (a)			2010 (b)		
Themisto libellula	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3	47 (10 – 82)	49 (27 – 71)	54 (38 – 72)	41 (5 – 80)	54 (30 – 79)	56 (37 – 77)
16:1n-7, 20:5n-3	49 (11 – 90)	53 (28 – 81)	59 (39 – 80)	43 (4 – 83)	58 (29 – 87)	52 (32 – 74)
20:5n-3, 22:6n-3	49 (9 – 88)	47 (18 – 77)	55 (32 – 78)	45 (4 – 86)	48 (15 – 80)	60 (39 – 82)
20:5n-3	51 (10 – 95)	53 (19 – 93)	63 (34 – 96)	48 (6 – 94)	50 (15 – 91)	63 (35 – 96)
	2009 (a)			2009 (b)		
Calanus marshallae/glacialis	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3	48 (7 – 82)	50 (28 – 71)	39 (0 – 74)	48 (4 – 87)	53 (23 – 81)	39 (0 – 77)
16:1n-7, 20:5n-3	30 (1 – 61)	36 (14 – 59)	31 (0 –69)	28 (1 – 60)	36 (11 – 60)	32 (0 – 70)
20:5n-3, 22:6n-3	63 (36 – 96)	63 (42 – 85)	50 (10 – 91)	68 (39 – 98)	70 (49 – 92)	53 (10 – 95)
20:5n-3	56 (25 – 94)	55 (29 – 86)	44 (2 – 85)	57 (25 – 94)	56 (30 – 88)	44 (2 – 85)
	2010 (a)			2010 (b)		
Calanus marshallae/glacialis	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3	49 (22 – 77)	27 (8 – 47)	42 (5 – 79)	40 (12 – 69)	34 (12 – 56)	45 (7 – 81)
16:1n-7, 20:5n-3	52 (26 – 82)	30 (7 – 53)	47 (5 – 87)	39 (10 – 73)	37 (9 – 60)	44 (4 – 85)
20:5n-3, 22:6n-3	51 (17 – 85)	31 (4 – 56)	48 (5 – 87)	45 (11 – 80)	30 (2 – 56)	50 (8 – 88)
20:5n-3	57 (25 – 96)	39 (2 – 71)	54 (12 – 98)	47 (11 – 88)	36 (1 – 69)	54 (13 – 98)
	2009 (a)			2009 (b)		
Thysanoessa raschii	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3	48 (11 – 87)	64 (39 – 92)	46 (4 – 84)	49 (10 – 91)	68 (40 – 97)	46 (3 – 86)
16:1n-7, 20:5n-3	42 (5 – 78)	54 (29 – 85)	39 (0 – 78)	42 (4 – 80)	55 (26 – 87)	39 (0 – 79)
20:5n-3, 22:6n-3	56 (19 – 97)	71 (47 – 99)	55 (13 – 97)	58 (19 – 99)	76 (50 – 100)	56 (13 – 98)
20:5n-3	49 (8 – 93)	60 (28 – 98)	48 (3 – 91)	50 (9 – 94)	61 (30 – 99)	48 (2 – 92)
	2010 (a)			2010 (b)		
Thysanoessa raschii	Max Ice	Ice Melt	Ice-Free	Max Ice	Ice Melt	Ice-Free
16:1n-7, 20:5n-3, 22:6n-3	45 (1 – 88)	49 (26 – 72)	57 (25 – 96)	46 (1 – 90)	54 (29 – 78)	59 (26 – 97)
16:1n-7, 20:5n-3	46 (1 – 91)	53 (21 – 81)	58 (21 – 99)	48 (2 – 93)	56 (29 – 86)	56 (21 – 98)
20:5n-3, 22:6n-3	47 (2 – 91)	50 (19 – 82)	57 (20 – 98)	48 (2 – 92)	50 (15 – 84)	59 (21 – 99)
20:5n-3	48 (3 – 93)	56 (23 – 96)	56 (12 – 99)	49 (3 – 94)	53 (19 – 93)	57 (15 – 99)

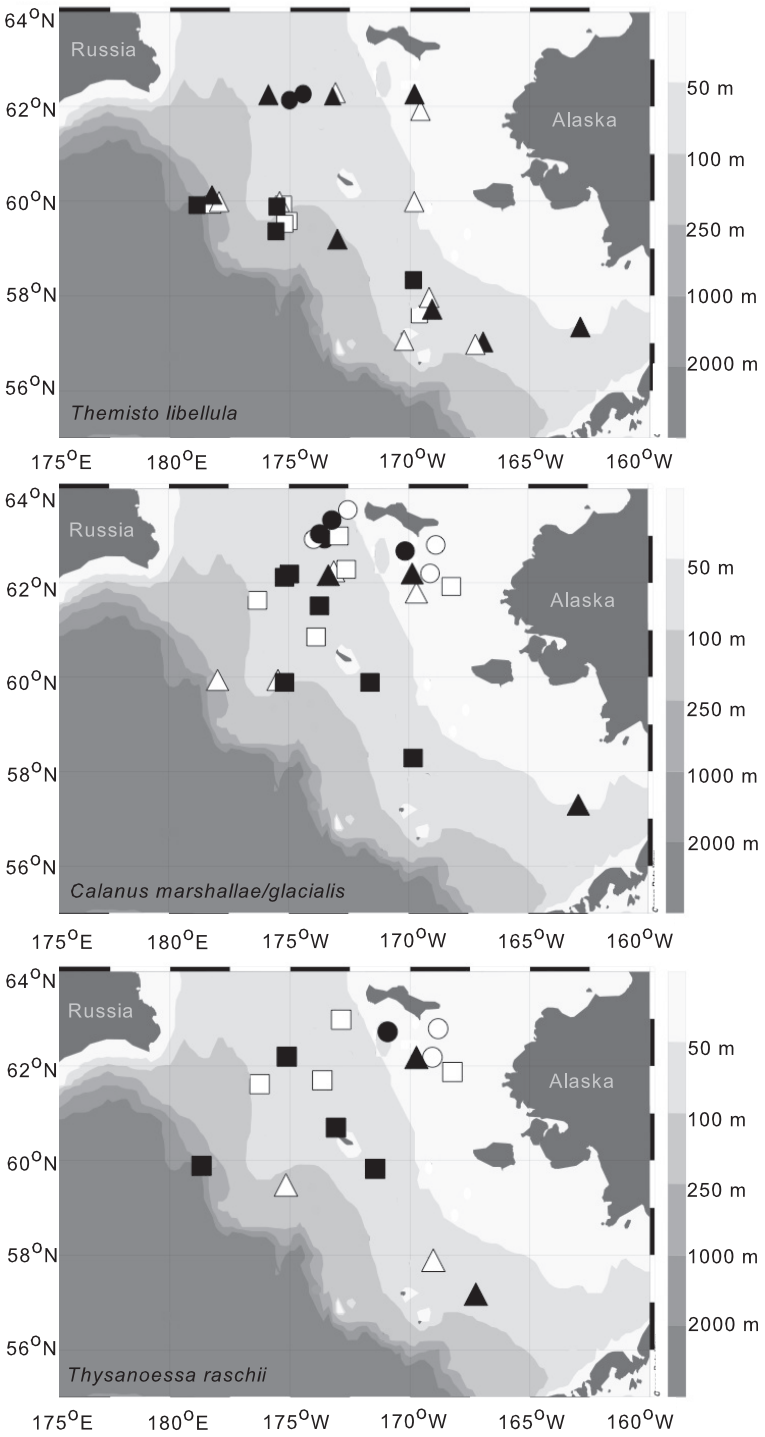


Figure 2.1. Sampling stations for *Themisto libellula, Calanus marshallae/glacialis,* and *Thysanoessa raschii.* Samples were collected during maximum ice extent (circles), ice melt (squares), and ice-free conditions (triangles) in 2009 (open symbols) and 2010 (shaded symbols). *T. libellula* samples were not collected during maximum ice extent in 2009. Details for sampling stations and sample sizes are given in Appendix 2.1

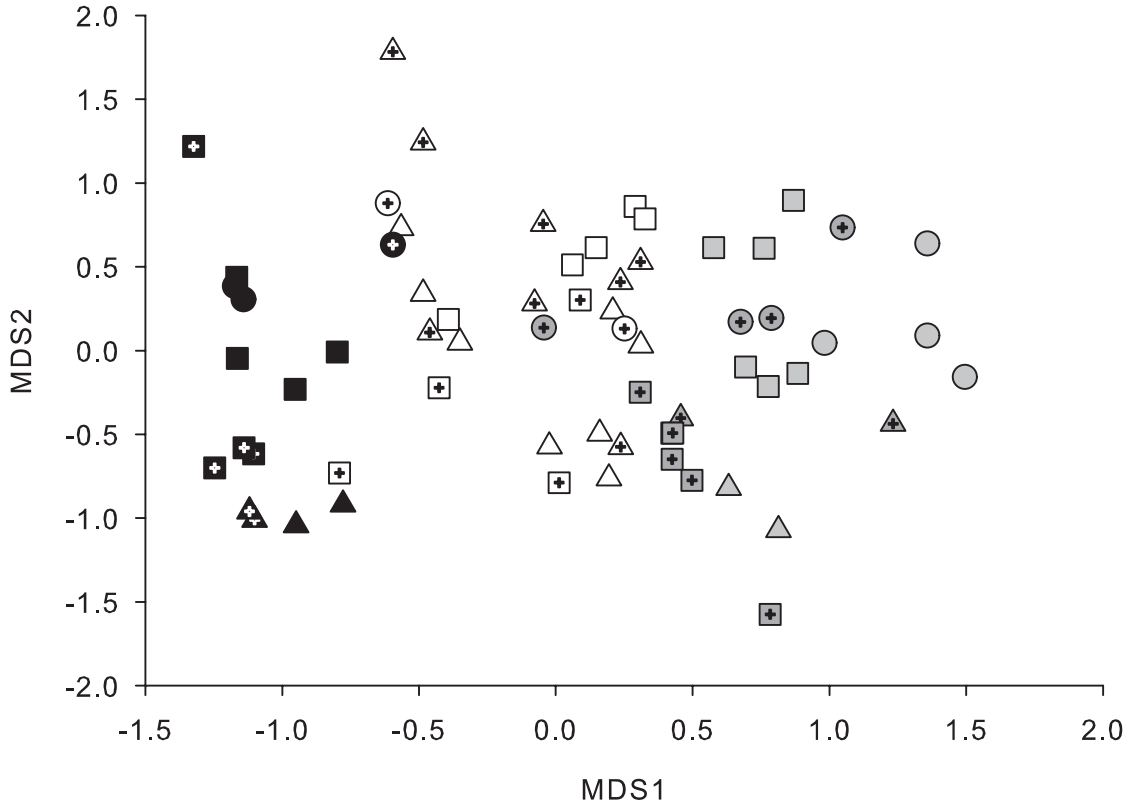


Figure 2.2. nMDS plot of *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii*. Analysis used 63 fatty acids present in proportions >0.1%. Samples were collected in 2009 and 2010 during maximum ice extent (circles), ice melt (squares), and ice-free conditions (triangles). *T. libellula* samples were not collected during maximum ice extent in 2009. 2D stress=0.12. *Themisto libellula* = open symbols, *Calanus marshallae/glacialis* = shaded symbols, *Thysanoessa raschii* = closed symbols. Samples collected in 2009 are represented by the solid symbols, 2010 are represented by symbols with '+' inside

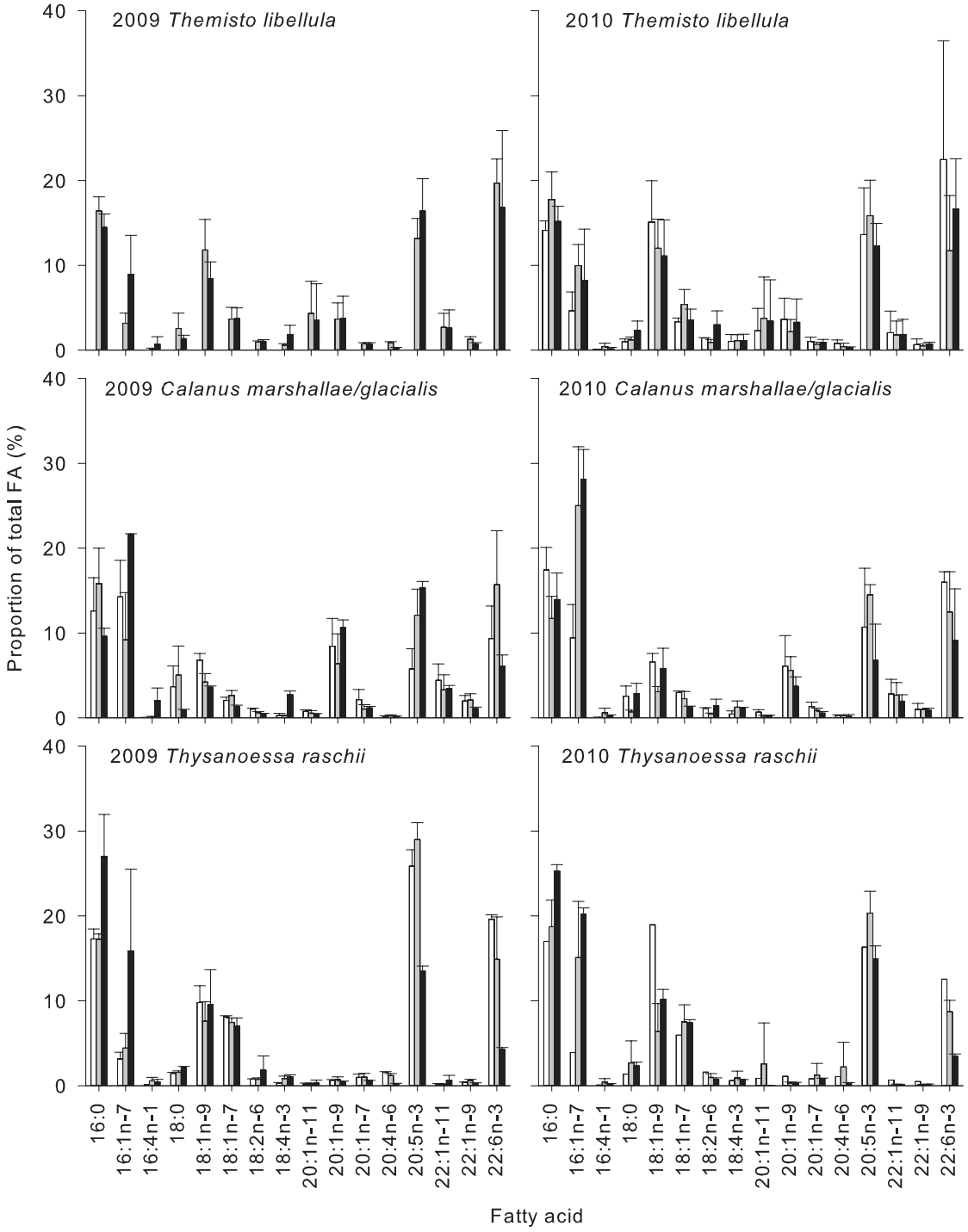


Figure 2.3. Proportions of select fatty acids in *Themisto libellula*, *Calanus marshallae/glacialis*, and *Thysanoessa raschii.* Samples were collected during maximum ice extent (open bars), ice melt (shaded bars) and ice-free conditions (filled bars) in 2009 and 2010 from the Bering Sea (mean + 1SD). *T. libellula* samples were not collected during maximum ice extent in 2009

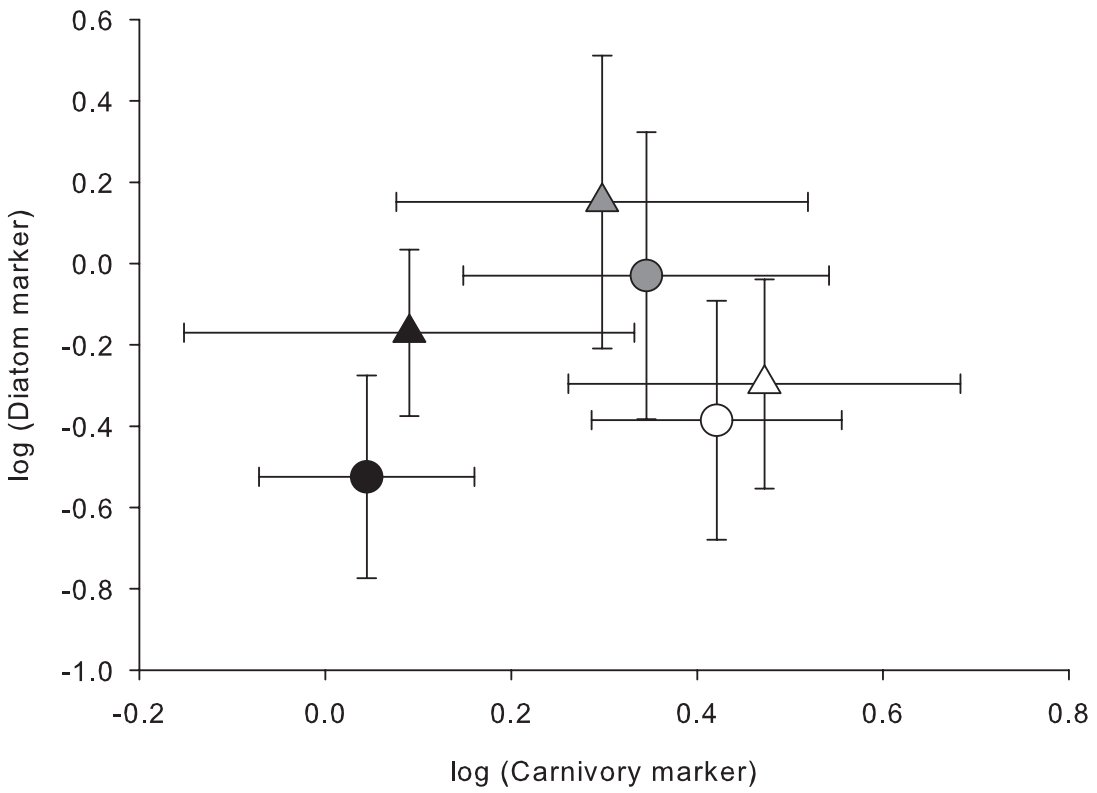


Figure 2.4. Biplot of the carnivory marker (18:1n-9/18:1n-7) and the diatom marker (16:1/16:0) for *Themisto libellula, Calanus marshallae/glacialis*, and *Thysanoessa raschii. T. libellula*=open symbols, *C. marshallae/glacialis*=shaded symbols, and *T. raschii*=closed symbols. Samples in 2009=circles and 2010=triangles (mean ± 1SD). Samples were pooled by species

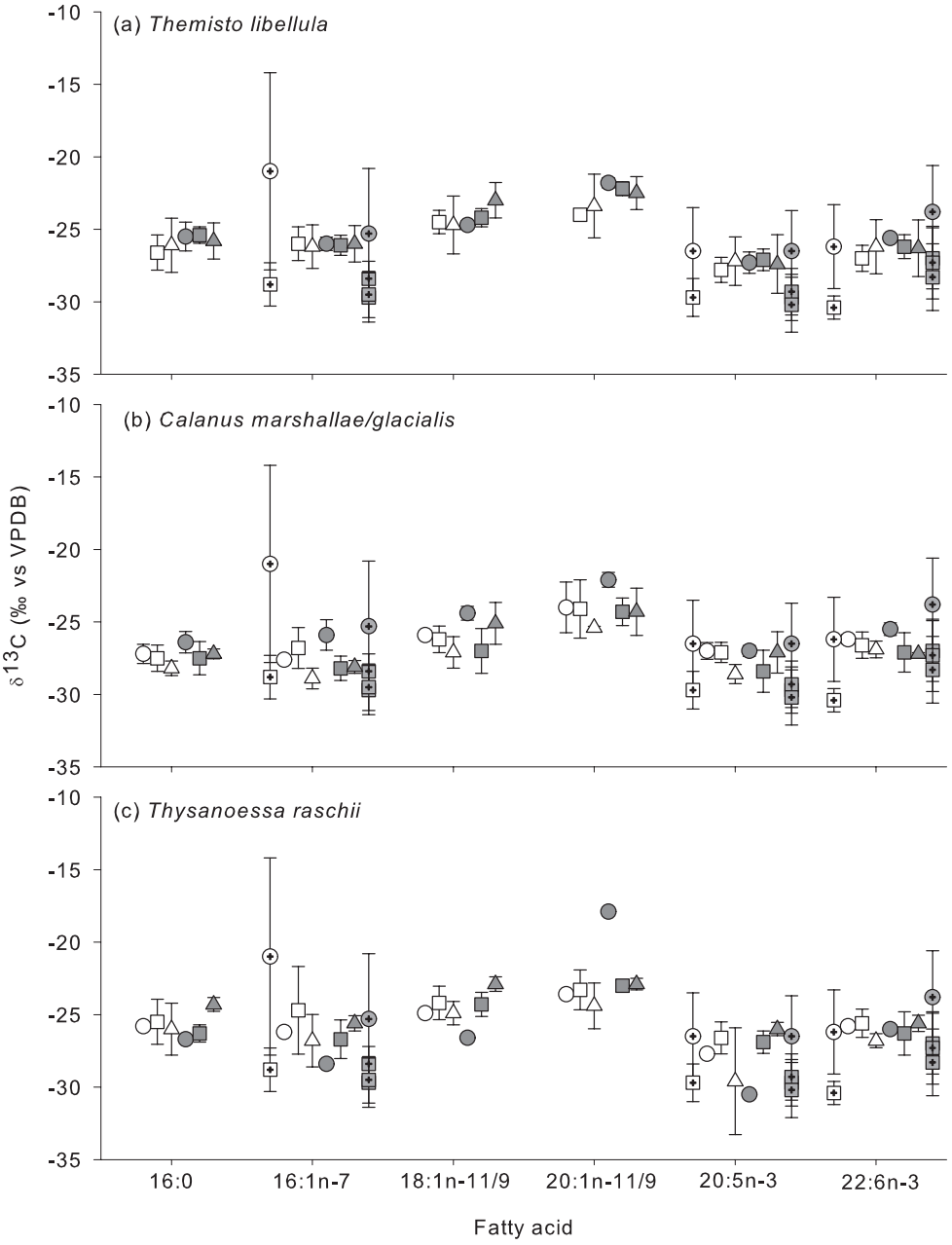


Figure 2.5. $\delta^{13}C$ values for six fatty acids in (a) *Themisto libellula,* (b) *Calanus marshallae/glacialis*, and (c) *Thysanoessa raschii.* Samples were collected during maximum ice extent (circles), ice melt (squares), and ice-free conditions (triangles) in 2009 (open symbols) and 2010 (closed symbols) from the Bering Sea. *T. libellula* samples were not collected during maximum ice extent in 2009. $\delta^{13}C$ values for 16:1n-7, 20:5n-3, and 22:6n-3 from i-POM and p-POM from 2009 and 2010 are also shown for comparison. In 2009, i-POM (open circle with '+' inside) and p-POM (open square with '+' inside) samples were collected only during ice melt conditions. In 2010, i-POM samples were collected during maximum ice extent (closed circle with '+' inside), and p-POM samples were collected during maximum ice extent, ice melt, and ice-free conditions (n=3 closed squares with '+' inside). Mean ± 1SD

Appendix 2.1. Sample information for (a) *Themisto libellula*, (b) *Calanus* marshallae/glacialis, and (c) *Thysanoessa raschii* collected from the Bering Sea in 2009 and 2010. Samples were collected during maximum ice, ice melt, and ice-free conditions. *T. libellula* samples were not collected during maximum ice conditions in 2009.

(a) *Themisto libellula*

Cruise, Ice conditions	Date (m/dd/yyyy)	Station no.	Station name	Latitude °N	Longitude °W	No. individuals
HLY0902, Ice melt (n=5)	4/10/2009	19	MN13	59.876	-175.215	1
	4/12/2009	25	MN19	59.901	-178.908	4
	4/22/2009	58	NP9	57.445	-169.754	1
	4/29/2009	69	BL1	59.537	-175.205	1
	4/29/2009	85	BL15	59.55	-175.096	1
KNORR195-10, Ice-free (n=8)	6/20/2009	32	CNN6	56.787	-167.874	2
	6/22/2009	49	NP11	56.983	-170.288	3
	6/22/2009	45	NP7	57.911	-169.248	5
	7/01/2009	98	MN4	59.910	-169.803	2
	7/02/2009	108	MN13	59.913	-175.206	2
	7/03/2009	114	MN18	59.910	-178.206	3
	7/06/2009	133	SLN2	61.868	-169.876	6
	7/07/2009	140	SL9	62.202	-173.118	3
PSEA10-01, Max ice (n=2)	3/13/2010	1	VNG-1	62.046	-175.067	1
	3/14/2010	3	NWC-4	62.418	-174.696	1
TN249, Ice melt (n=4)	5/17/2010	39	IE1	59.337	-175.611	15
	5/19/2010	49	MN19	59.911	-178.953	10
	5/27/2010	81	70m26	58.175	-169.907	1
	6/08/2010	170	MN13	59.901	-175.202	3
TN250, Ice-free (n=8)	6/15/2010	45	NP7	57.889	-169.223	1
	6/19/2010	18	CN4	57.279	-162.923	9
	6/23/2010	33	CNN5	57.052	-167.449	1
	6/29/2010	69	P14-N4	58.960	-173.873	6
	7/03/2010	99	MN18	59.900	-178.200	4
	7/06/2010	124	SL1	62.200	-169.849	1
	7/06/2010	132	SL9	62.200	-173.116	1
	7/07/2010	139	SL16	62.200	-175.905	1

(b) *Calanus marshallae/glacialis*

Cruise, Ice conditions, n	Date (m/dd/yyyy)	Station no.	Station name	Latitude °N	Longitude °W	No. individuals
HLY0901, Max ice (n=4)	3/18/2009	8	08NWC1	63.705	-172.540	15
	3/24/2009	24	24WAL12	62.125	-169.250	10
	3/26/2009	36	36MK1B	62.847	-169.022	16
	3/28/2009	41	41NWC3	62.912	-174.069	30
HLY0902, Ice melt (n=6)	4/14/2009	29	St. 29	61.792	-176.802	8
	4/16/2009	35	SL 9	63.094	-173.291	8
	4/18/2009	45	SL1	61.958	-167.991	7
	4/28/2009	83	St. 83	60.821	-174.384	12
	5/01/2009	92	St. 92	61.589	-173.709	8
	5/02/2009	93	BN1	62.333	-172.703	8
KNORR195-10, Ice-free (n=2)	7/06/2009	133	SLN2	61.868	-169.876	12
	7/07/2009	140	SL9	62.202	-173.118	15
PSEA10-01, Max ice (n=4)	3/16/2010	8	VNG-4	62.946	-173.461	20
	3/21/2010	26	NEC2	62.612	-170.166	20
	3/25/2010	41	NWC-3	62.971	-173.941	15
	3/28/2010	47	NWC-2	63.354	-173.221	8
TN249, Ice melt (n=6)	5/27/2010	81	70m26	58.175	-169.907	30
	6/03/2010	134	70m39	59.846	-171.838	40
	6/04/2010	147	70m52	61.418	-173.736	30
	6/05/2010	156	SL12	62.193	-175.155	20
	6/05/2010	158	SL9	62.104	-175.291	30
	6/08/2010	170	MN13	59.901	-175.202	40
TN250, Ice-free (n=2)	7/06/2010	124	SL1	62.200	-169.849	10
	7/06/2010	132	SL9	62.200	-173.116	10

(c) *Thysanoessa raschii*

Cruise, Ice conditions, n	Date (m/dd/yyyy)	Station no.	Station name	Latitude °N	Longitude °W	No. individuals
HLY0901, Max ice (n=2)	3/23/2009	21	21MK1	62.969	-169.156	8

Appendix 2.1. Continued…

	3/24/2009	24	24WAL12	62.125	-169.250	10
HLY0902, Ice melt (n=4)	4/14/2009	29	St. 29	61.792	-176.802	4
	4/16/2009	35	SL 9	63.094	-173.291	6
	4/18/2009	45	SL1	61.958	-167.991	4
	5/01/2009	92	St. 92	61.589	-173.709	2
KNORR195-10, Ice-free (n=2)	6/22/2009	45	NP7	57.911	-169.248	1
	7/05/2009	122	XB2-12	59.573	-175.250	1
PSEA10-01, Max ice (n=1)	3/23/2010	37	CD10-D	62.832	-171.42	3
TN249, Ice melt (n=4)	5/19/2010	49	MN19	59.911	-178.953	3
	6/03/2010	134	70m39	59.846	-171.838	6
	6/04/2010	147	70m52	61.418	-173.736	4
	6/05/2010	156	SL12	62.193	-175.155	4
TN250, Ice-free (n=2)	6/23/2010	33	CNN5	57.052	-167.449	2

approved

Rolf Gradinger
Associate Dean
School of Fisheries and Ocean Sciences
252 O Neill Building
Fairbanks AK 99775-7220

907 474 7407

http://www.sfos.uaf.edu/research/seaicebiota/
http://scholar.google.com/citations?user=1RKfeo0AAAAJ&hl=en

On 4/11/14 2:22 PM, Shiway Wang wrote:

> HI Rolf!
>
> Because you are not on my committee but are a coauthor, I need your permission to include the following papers in my dissertation:
>
> (Chapter 1) Wang SW, Budge SM, Gradinger RR, Iken K, Wooller (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699-712
>
> and
>
> (Chapter 2) Wang SW, Budge SM, Iken K, Gradinger RR, Wooller MJ. Zooplankton diets in the Bering Sea inferred using fatty acid and compound-specific stable isotope analyses reveal the relative importance of pelagic and sympagic carbon sources. In Review. Marine Ecology Progress Series
>
> Will you grant me permission to include these papers in my dissertation? :)
>
> thanks!
> Shiway
>
> --
> Shiway Wang
> MS Marine Biology
> PhD Candidate
> School of Fisheries & Ocean Sciences
> University of Alaska Fairbanks
> shiway@gmail.com
> (907) 460 2496
> https://www.sfos.uaf.edu/people/profile.php?uid=2160

Appendix 2.2 Permission to use manuscript in thesis from Rolf Gradinger

CHAPTER 3:

Trophic relationships and carbon sources of ice seals during recent environmental shifts in the Bering Sea[1]

Abstract

Dramatic multiyear fluctuations in seasonal sea ice extent and duration across the Bering-Chukchi continental shelf have occurred in this century. A pressing ecological question is thus raised: do such changes alter marine production processes linking primary producers to upper trophic level predators? We examined this question by comparing the blubber fatty acid (FA) composition of adult ringed (*Pusa*/*Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*), collectively known as 'ice seals,' sampled during the Bering Sea warm, low sea ice period (2002 – 2005) and a following cold, relatively high sea ice period (2007 – 2010). The FA composition of ice seals showed clear evidence of resource partitioning among ringed, bearded, and spotted seals, and little niche separation between spotted and ribbon seals, which is consistent with previous studies. The FA composition of primarily pelagic feeding ringed seals and primarily benthic feeding bearded seals did not differ between the recent warm and cold periods in the Bering Sea, suggesting that their diets were not affected by these large multiyear environmental fluctuations. We also used carbon stable isotope values of individual FAs ($\delta^{13}C_{FA}$) to estimate the contribution of sympagic organic matter to seals relative to organic matter derived from water column phytoplankton. Estimates from mixing models indicated that bearded seals had the highest contribution of FAs originating from sympagic organic matter (62 – 80%), followed by spotted seals (51 – 62%), and then ringed seals (21 – 60%) in 2009 and 2010. These values suggest that sympagic production currently is an important contributor to food webs supporting these pinnipeds. Notably, the $\delta^{13}C_{FA}$ values of bearded seals were higher during the Bering Sea cold period than the warm period, suggesting that the sources of primary production of their prey switched to more sympagic sources. Thus, important concerns are raised – the projected continuing loss of seasonal sea ice in the Arctic, the subsequent decline of organic matter input from sympagic production, and if it will be compensated for by pelagic production to balance both pelagic and benthic carbon and energy budgets.

[1] Prepared for submission to Functional Ecology as Wang SW, Budge SM, Horstmann-Dehn L, Quakenbush LT, Springer AM, Wooller MJ. Trophic relationships and carbon sources of ice seals during recent environmental shifts in the Bering Sea

Introduction

The Arctic has warmed at nearly twice the rate of the rest of the world in recent decades, and the trend is projected to continue through this century with a nearly sea ice-free Arctic in September by the year 2037 (ACIA 2004, Wang & Overland 2009, 2012). Arctic sea ice extent has decreased in virtually all regions since the beginning of the satellite record, with the exception of the Bering Sea during winter (Perovich et al. 2013). In the Bering Sea, dramatic multiyear fluctuations in sea ice extent have occurred, alternating between cold years characterized by extensive spring sea ice extent and warm years with relatively lower spring ice extent (Stabeno et al. 2001, 2007, 2012a, Stabeno & Hunt Jr 2002). The most recent warm period in the Bering Sea was between 2001 and 2005 and was followed by a cold period since 2007 and is currently ongoing (NSIDC 2011, Stabeno et al. 2012a).

The extent of sea ice and the timing of the spring ice retreat affect the timing of spring phytoplankton blooms, which can be seeded by sea ice algae (e.g., Spindler 1994, Bluhm & Gradinger 2008). The reduction in seasonal sea ice has increased the net primary productivity by 30% in the Chirikov Basin in the northern Bering Sea and by 20% in the Arctic Ocean over a recent 12-year period (Brown & Arrigo 2012). In addition, a previously undocumented under-ice pelagic diatom bloom was observed in July 2011 in the Chukchi Sea that was most likely influenced by increased early light penetration through thinning sea ice cover and melt water pools on the ice (Arrigo et al. 2012, 2014). These changes in the timing and quantity of primary production by sea ice algae and pelagic phytoplankton could alter food web ecosystem dynamics in the Arctic (Hunt et al. 2002, Grebmeier et al. 2006, Bluhm & Gradinger 2008, Leu et al. 2011, Grebmeier 2012, Søreide et al. 2013). Consequently, such changes in the ecosystem may in turn affect the diets of higher trophic level predators such as ringed (*Pusa* or *Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*), collectively known as 'ice seals' because of their strong associations with the sea ice habitat. In part because of potential changes in diet due to sea ice loss from climate change, and consequences to individual and population health, the Arctic Basin population of ringed seals and the Pacific population of bearded seals were listed as threatened under the provisions of the U.S. Endangered Species Act in 2012 (NMFS 2012a, b).

The feeding ecology and habitat preferences of ice seals differ among species within the sea ice environment (e.g., Simpkins et al. 2003). Ringed seals are found in heavy ice including coastal land-fast ice and primarily consume Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), and crustaceans (e.g., gammarid amhipods and shrimp) (McLaren 1958, Lowry et al. 1980a, Dehn et al. 2007, Quakenbush et al. 2011a). In a recent

study, satellite tagged adult ringed seals from Kotzebue Sound, Alaska remained in the northern Bering and Chukchi Seas in the winter-spring season on shorefast or heavy pack ice to maintain breeding territories (Crawford et al. 2012). In contrast, bearded seals predominately feed on benthic organisms, typically avoid heavy ice cover, and are found in drifting pack ice in relatively shallow shelf waters (Lowry et al. 1980b, Burns et al. 1981, Simpkins et al. 2003, Dehn et al. 2007). However, bearded seals also feed on pelagic prey, possibly when benthic prey are not available (e.g., Finley & Evans 1983, Antonelis et al. 1994, Dehn et al. 2007, Carroll et al. 2013). Bearded seals from the Bering Sea seasonally migrate north to Arctic seas but winter and breed in the Bering Sea (http://kotzebueira.org/environmental-projects/young-bearded-seal/index.html). Spotted seals tend to stay near the southern ice edge and avoid regions of thicker ice in winter and spring, but they spend the summer in coastal waters often hauling out on land (Fay 1974, Burns 2002). Satellite tagged Alaskan spotted seals were found to spend January-June 100-200 km off shore and were widely distributed in the region north of the 200-m isobath in the Bering Sea, while during August-October they were found generally nearshore (Lowry et al. 2000). Spotted seals feed primarily on fishes but also crustaceans and cephalopods (e.g., Bukhtiyarov et al. 1984, Dehn et al. 2007, Quakenbush et al. 2009). Ribbon seals are also found in the southern seasonal pack ice during the breeding season in late April through early May (Burns 1971, Fay 1974, Lowry 1985, Kelly 1988) and consume a range of pelagic and benthic prey such as shrimps, crabs, mysids, cephalopods, and fishes including walleye pollock (*Theragra chalcogramma*), eelpout (*Lycodes* spp.), capelin (*Mallotus villosus*), Arctic cod, and saffron cod (e.g., Burns 1971, Frost & Lowry 1980, Ziel et al. 2008).

In this study, we used the fatty acid (FA) composition of ice seals in Alaska to: 1) determine if diets changed seasonally within species (spring-summer versus fall-winter months), 2) examine the inter-annual variability within species (among the years 2002 – 2010), and 3) assess if diets differed between the recent warm and cold period in the Bering Sea. FA analysis has been used widely to study the diets of marine mammals (e.g., Iverson et al. 1997a, Walton et al. 2000, Walton & Pomeroy 2003, Beck et al. 2007, Thiemann et al. 2007, 2008, Cooper et al. 2009) and provides longer-term qualitative diet information than stomach content analysis (e.g., Iverson et al. 1997a). We estimated the contribution of pelagic and sympagic FAs to ice seal blubber during 2009 and 2010 using the carbon stable isotopes of individual FAs ($\delta^{13}C_{FA}$ values) from sea ice-derived organic matter (i-POM) and pelagic-derived POM (p-POM). $\delta^{13}C_{FA}$ values have been used previously to estimate the proportion of sympagic FAs relative to pelagic FAs in consumers in the marine Arctic and sub-Arctic (Budge et al. 2008, Graham

et al. 2014). This method is possible because $\delta^{13}C_{FA}$ of sea ice algae and i-POM have higher $\delta^{13}C_{FA}$ values than those of pelagic phytoplankton and p-POM (Budge et al. 2008, Wang et al. 2014 – referred from here on as Chapter 1 in this dissertation). In addition, inferences were made of the proportions of FAs from i-POM versus p-POM from $\delta^{13}C_{FA}$ values found in seals sampled during the recent warm and cold periods in the Bering Sea. By combining stable isotope analysis with FA analysis, more detailed information on pathways of carbon and energy transfer through food webs can be obtained.

Methods

Sample collection

Full-thickness blubber samples (skin to muscle) of adult ice seals (≥ 5 years of age) were collected from unknown locations from the trunk of the body. Ages of seals were estimated by counting cementum growth layers of sectioned teeth (Matson's Laboratory, Montana, USA), with one growth layer group representing one year of age (Mansfield & Fisher 1960, Benjaminsen 1973, Stewart et al. 1996). All samples were obtained opportunistically from the Alaskan Native subsistence hunts near the coastal communities, from south to north, of Hooper Bay, Gambell, Savoonga, Nome, and Little Diomede in the Bering Sea, and Shishmaref, Kivalina, and Point Hope in the Chukchi Sea (Fig. 3.1). Ringed seal samples were collected in 2003 through 2010, bearded seal samples were collected in 2002 through 2010, spotted seal samples were collected in 2003 through 2009, and ribbon seal samples were collected in 2003 and in 2008 (Table 3.1). The adult bearded seal FA data from 2002 were from Budge et al. (2007), and some of the FA data for all adult ice seals from 2003 were from Cooper et al. (2009). Sample sizes by season, year, and location are given in Appendix 3.1. FA data for 61 bearded seals in this study were also used in a comparison of diet analysis techniques by Bryan (2014). The random sampling of blubber was assumed to not affect the analyses, because blubber FA composition of pinnipeds is uniform across the body (Koopman et al. 1996, Cooper 2004, Lambert et al. 2013). Samples were collected as soon as possible after death and archived at -20°C. Sub-samples were taken using a clean scalpel and glass cutting board. Any oxidized tissue was removed, then the sample was wrapped tightly in aluminum foil and frozen at -80°C in air-tight bags until analysis. Actual timing of harvest, sample collection, and sample size was dependent on ice and weather conditions and seal availability. Sample sizes are given in Table 3.1. All samples were collected as part of the Alaska Department of Fish and

Game's ongoing biomonitoring program under National Marine Fisheries Service Scientific Research Permit No. 358-1787.

Laboratory analysis

A longitudinal slice (500 mg) of full-thickness blubber was sub-sampled, and any skin and muscle were removed. Lipids were extracted from all samples using 2:1 chloroform/methanol (Folch et al. 1957, Parrish 1999). Fatty acid methyl esters (FAME) were prepared using an acidic transesterification procedure (Budge et al. 2006). FAME were quantified using temperature-programmed gas chromatography (GC) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30 m x 0.25 mm internal diameter column coated with 50% cyanopropyl- methylpolysiloxane (DB-23) and linked to a computerized integration system (Varian Star software) at Dalhousie University according to Budge et al. (2006). Shorthand nomenclature of A:Bn-X was used to describe each FAME, where A represents the number of carbon atoms, B the number of double bonds, n represents the terminal methyl group, and X the position of the double bond closest to the terminal methyl group. For non-methylene interrupted (NMI) FAs, nomenclature of A:BΔX,Y,Z was used, where A, B, and X are defined as above, Δ represents the terminal methyl group, and Y and Z (if applicable) represent the position of the double bonds from the terminal methyl group. Up to 76 FAME were identified by comparison of retention times with known standards (Nu Check Prep, Elysian, MN, USA) or by using GC-mass spectrometry (Appendix 3.2).

Carbon stable isotope ratios (expressed as $\delta^{13}C$ values in per mil - ‰) of individual FAME were analyzed by routing the effluent from a GC (Trace GC Ultra, Bremen, Germany) through a combustion interface (Finnigan GC combustion III, Bremen, Germany) to an isotope ratio mass spectrometer (IRMS) (Thermo Finnigan Delta V, Bremen, Germany) at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. The same GC column and method described above for FID analyses of FAME were used to separate the FAME for carbon stable isotope analysis using GC-IRMS (Budge et al. 2008, 2011, Chapter 1). The $\delta^{13}C$ values from the individual FAMEs were calibrated using a standard mixture consisting of ethyl and methyl esters of 14:0, 16:0, 18:0, and 20:0 (supplied by Indiana University Stable Isotope Reference Materials), where the coefficient of determination (r^2) of the measured versus expected relationship was >0.97. 16:0 and 18:0 FAME laboratory standards were analyzed after every ten samples to track analytical error of the GC-IRMS system, which was ≤0.3 ‰ (representing 1 standard deviation-SD of 53 analyses of the 16:0 and 18:0 standards interspersed during the sample runs). All $\delta^{13}C$ values were reported

relative to Vienna Pee Dee Belemnite (VPDB) using standard notation, where $\delta^{13}C$ (‰) = [($R_{sample}/R_{standard}$) – 1] x 1000, and R is the corresponding ratio of $^{13}C/^{12}C$.

Data analysis

Seals were harvested throughout the year, and months were grouped in two periods, the time of reduced feeding (April through August, referred to as spring-summer) and feeding (September through March, referred to as fall-winter) (McLaren 1958, Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010, Quakenbush et al. 2011a, b, Carroll et al. 2013). Stable isotope ratios and stomach contents can be different among age classes within ice seal species (Dehn et al. 2007, Quakenbush et al. 2011 a, b). Thus, we limited our analyses to samples from adult animals (≥5 years) from locations in the Bering and Chukchi Seas in this study to remove any variation due to age, although there is evidence that FA profiles do not differ among age classes in ice seals (Budge et al. 2007, Cooper et al. 2009). Additionally, there is little evidence for differences in FA profiles due to sex in adult ice seals (Budge et al. 2007, Thiemann et al. 2007, Cooper et al. 2009). There is some indication from stomach content analysis that within species (ringed, bearded, and spotted seals) diets did not differ by sex, but did differ among seals foraging in the Bering and Chukchi Seas within species (Lowry et al. 1980a, b, Quakenbush et al. 2009, 2011a, b). For bearded seals, we were able to compare a subset of FA profiles between samples collected during spring-summer on Little Diomede (Bering Sea) and Point Hope (Chukchi Sea) in 2005, 2007, 2009, and 2010. However, sample sizes did not allow for the comparison of FA profiles among sampling locations within years for ringed, spotted, and ribbon seals (e.g., spotted seal samples in 2004 were only collected from Shishmaref, Table 3.1). Thus, we pooled all samples by seasons, sex, and location to make comparisons within species by year. To determine if the diets of ringed and bearded seals were different between the warm and cold year periods in the Bering Sea, samples were pooled from 2003 – 2005 for ringed seals and 2002 – 2005 for bearded seals to represent diets from the Bering Sea warm years, and pooled from 2007 – 2010 to represent diets during the Bering Sea cold years (Stabeno et al. 2012a). The year 2006 was not included in the warm and cold period comparisons because it is considered a transition year in the Bering Sea (Stabeno et al. 2012a). To make comparisons among ice seal species, samples were pooled by species across all years, sexes, seasons, and locations. Individuals of all species are highly mobile (e.g., Crawford et al. 2012) and considered to be part of the same population within the Bering and Chukchi Seas (Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010). Consequently, any inferences made are based at the population level

for each species regardless of potential differences among locations. Groups with only one sample were not included in the data analyses (Table 3.1).

FA data often violate the assumptions for parametric methods (i.e., normality, independence, and equality of covariance matrices); thus, we used non-parametric multivariate methods from PRIMER 6 (PRIMER-E Ltd; Clarke & Warwick 2001; Clarke & Gorley 2006) and a Kruskal-Wallis Analysis of Variance (ANOVA) to analyze FA data. Bray-Curtis similarity matrices and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) were used to investigate the variation in FA compositions of ice seals, based on the 48 FAs present in proportions >0.1% (means and 1 SD for each species are given in Appendix 3.2). Distance-based redundancy analysis (dbRDA; McArdle & Anderson 2001) was used to visualize differences among FA profiles and assess the contribution of FAs to the variation observed among species. In addition to PERMANOVA, similarity percentages routines (SIMPER) were performed to determine the FAs contributing most to the observed differences among species and any variation among years, and between fall-winter and spring-summer months within species. Non-metric scaling (nMDS) plots were used to visualize differences between FA profiles during Bering Sea warm and cold years for ringed and bearded seals. FA data were standardized to 100% and log (X+1) transformed prior to analysis to down weigh the FAs present in higher proportions and increase the weighting of FAs present in lower proportions. A Kruskal–Wallis ANOVA was used to test for differences of individual non-methylene interrupted (NMI) FAs (20:2Δ5,11; 20:2Δ5,13; 20:3Δ5,11,14; 22:2NMID; 22:2Δ7,13, and 22:2Δ7,15) among species. A Mann-Whitney U-test was used to compare NMI FA levels between warm and cold years in the Bering Sea for ringed and bearded seals.

Because the $\delta^{13}C_{FA}$ data also violated some of the assumptions for parametric statistics, we used the same non-parametric multivariate methods mentioned above to analyze $\delta^{13}C_{FA}$ data. Not all FAs were present in sufficient analytical quantities to determine their respective $\delta^{13}C_{FA}$ values. $\delta^{13}C_{FA}$ values were determined for 14:0, 18:1n-11/9, 18:1n-7, and 18:2n-6 in all samples. Additionally, $\delta^{13}C_{FA}$ values could be determined for 16:0, 16:1n-7, 18:4n-3, 20:1n-11/9, 20:5n-3, 22:5n-3, and 22:6n-3 in all but eight samples (ringed seal *n*=1, bearded seal *n*=4, spotted seal *n*=2, ribbon seal *n*=1), and those samples were not used in the data analyses (Table 3.1). All FAs were well-resolved by GC-FID. Co-elution of two pairs of FAs (18:1n-11 and 18:1n-9; 20:1n-11 and 20:1n-9) occurred on the GC-IRMS and are referred to as 18:1n-11/9 and 20:1n-11/9, respectively. The $\delta^{13}C_{FA}$ values for these 11 FAs were transformed into Euclidean distances, and a PERMANOVA was used to investigate the variation in the $\delta^{13}C_{FA}$

values among species (ringed, bearded, spotted, ribbon seals), inter-annual variation within species (ringed, bearded, and spotted seals only), and seasonal variation within species (ringed and bearded seals only). A Kruskal–Wallis ANOVA was used to test for differences of individual $\delta^{13}C_{FA}$ values among species using STATISTICA version 12 (StatSoft, Inc. 2013). Statistical significance was determined using $\alpha = 0.05$.

We used a Bayesian multi-source stable isotope mixing model (SIAR, Parnell et al. 2010) to estimate the proportional contribution of i-POM and p-POM to ringed, bearded, and spotted seals in 2009, and ringed and bearded seals in 2010. The $\delta^{13}C_{FA}$ values for i-POM and p-POM were generated from the Bering Sea in 2009 (Chapter 2) and 2010 (Chapter 1, Chapter 2) and were used as the end member sources in our mixing models. Specifically, for ringed, bearded, and spotted seals sampled in 2009, mean i-POM and p-POM $\delta^{13}C_{FA}$ values of samples collected during ice melt between 14 April and 6 May 2009 (Chapter 2) were used as sources in the mixing models for seals sampled in April – August 2009 (spring-summer 2009) and September 2009 – March 2010 (fall-winter 2009). In 2010, the mean i-POM $\delta^{13}C_{FA}$ value from samples collected during maximum ice extent (13 – 28 March 2010; Chapter 1) was used as the i-POM source for ringed and bearded seals sampled in April – August 2010. Also in 2010, p-POM was collected from maximum ice extent (13 – 28 March), ice melt (11 May – 10 June 2010), and ice-free conditions (18 June – 10 July 2010). The p-POM $\delta^{13}C_{FA}$ values for FAs 20:5n-3 and 22:6n-3 did not differ by ice conditions (Chapter 1). Therefore, p-POM $\delta^{13}C_{FA}$ values for each FA were averaged across all ice conditions and used as the p-POM source in the model for ringed and bearded seals sampled in 2010. We used the diatom marker FA 20:5n-3 (e.g., Viso & Marty 1993) in the model, because the algal composition in i-POM is typically dominated by diatoms (Horner 1985, Gradinger 2002, Arrigo et al. 2010). The presence of diatoms was also found in p-POM in 2010 (Chapter 1). We also used the flagellate marker 22:6n-3 (e.g., Dalsgaard et al. 2003) in the model, because the water column can also contain non-diatom phytoplankton such as dinoflagellates and flagellates (Moran et al. 2012). To test the use of these different FA markers as indicators of i-POM and p-POM, we ran two mixing models using: (a) only the diatom FA 20:5n-3, and (b) 20:5n-3 and the flagellate marker FA 22:6n-3 as sources of i-POM and p-POM. Trophic enrichment factors were assumed to be zero (Budge et al. 2008, 2011). Models were run with and without concentration dependencies for comparison (Table 3.7). Results are presented as means and 95% credibility intervals (Bayesian confidence interval).

Results

Fatty acid profiles

FA profiles of ringed seals did not differ between seasons (spring-summer versus fall-winter) for the years 2005, 2007, 2008, and 2009 (PERMANOVA $P>0.311$, Table 3.2). There was some annual variation (PERMANOVA $P=0.009$, Table 3.3), although our small sample sizes likely limited and biased these comparisons somewhat (Table 3.1). FA profiles of bearded seals collected near Little Diomede in the Bering Sea differed from profiles of animals collected near Point Hope in the Chukchi Sea in 2005 and 2010, but not in 2007 and 2009 (PERMANOVA, see Table 3.4 for *P*-values). Within bearded seals, there was no seasonal variation (spring-summer vs. fall-winter) in FA profiles from 2004 (PERMANOVA $P=0.357$, Table 3.2). However, there was some annual variation with no consistent patterns in bearded seal FA profiles (PERMANOVA $P=0.025$, Table 3.3). Seasonal differences between FA profiles in spotted seals could not be analyzed due to sample size limitations, but there were a few differences in profiles among years (PERMANOVA $P=0.012$, Table 3.3). Results from SIMPER analyses of annual comparisons with FAs contributing to the differences among years within ringed, bearded, and spotted seals are given in Appendix 3.3. Seasonal and annual differences could not be examined for ribbon seals due to sample size limitations. Ringed seal FA profiles from samples collected during the warm period in the Bering Sea did not differ from those in the cold years (PERMANOVA $P=0.576$, Fig. 3.2). Similarly, FA profiles from bearded seals were not different between the Bering Sea warm and cold years (PERMANOVA $P=0.261$, Fig. 3.2). There was little variation between values of NMI FA in the Bering Sea warm and cold years for both ringed and bearded seals (Mann-Whitney U-test, see Table 3.5a for *P*-values, Fig. 3.3).

The variability in FA profiles was greater among species than within species (Fig. 3.4). FA profiles differed significantly among ringed, bearded, and spotted seals (PERMANOVA $P=0.001$). Spotted and ribbon seal FA profiles from spring-summer in 2003 were not different (PERMANOVA $P=0.066$). Ringed seal blubber had higher percentages of the PUFA 20:5n-3, 22:5n-3, and 22:6n-3 than the other species (dbRDA, Fig. 3.4). Ringed and bearded seals had high proportions of 16:1n-7, which distinguished them from spotted and ribbon seals (Fig. 3.5). Bearded seals were characterized also by higher proportions of 18:1n-7 and 20:1n-7 (dbRDA, Fig. 3.4). Spotted seals were characterized by higher proportions of 16:0, 20:1n-11, 20:1n-9, and 22:1n-11 than the other species (dbRDA, Fig. 3.5). Bearded seals had greater total proportions of NMI FAs (Appendix 3.2) and greater proportions of 20:2Δ5,11; 20:3Δ5,11,14; 22:2NMID; 22:2Δ7,13; and 22:2Δ7,15 compared with the other species. Ringed,

spotted, and ribbon seals did not differ from each other in the proportions of NMI FA, with the exception of 22:2Δ7,15, which was lower in ringed seals compared with spotted seals (Kruskal-Wallis ANOVA, see Table 3.5b for *P*-values, Fig. 3.6). FA data are provided in Appendix 3.2.

$\delta^{13}C_{FA}$ values of fatty acids

For ringed seals, there was no difference in $\delta^{13}C_{FA}$ between seasons (PERMANOVA P=0.561) or across years (PERMANOVA P=0.173). For bearded seals, $\delta^{13}C_{FA}$ values were not different between the spring-summer and fall-winter seasons in 2004, however, the small sample sizes likely limited this comparison (Table 3.1). The $\delta^{13}C_{FA}$ values from 2004 and 2005 were different from 2007 – 2010 (PERMANOVA, see Table 3.6 for *P*-values). Specifically, 8 of the 11 $\delta^{13}C_{FA}$ values (14:0, 16:0, 16:1n-7, 18:1n-11/9, 20:1n-11/9, 20:5n-3, 22:5n-3, and 22:6n-3) were significantly lower in bearded seals sampled in 2004 – 2005 than in bearded seals sampled in 2007 – 2010 (Mann-Whitney U-test, P<0.008, Fig. 3.7). Seasonal differences could not be analyzed for spotted or ribbon seals due to sample size limitations. $\delta^{13}C_{FA}$ of spotted seals collected during the fall-winter season differed among years (PERMANOVA P=0.025), but further pairwise comparisons showed a significant difference only between 2005 and 2008 (P=0.028, Table 3.6). In particular, $\delta^{13}C_{FA}$ values of 14:0, 16:0, 16:1n-7, 18:1n-11/9, 18:1n-7, 20:1n-11/9, 20:5n-3, and 22:6n-3) were significantly lower in spotted seals sampled in 2005 than in spotted seals sampled in 2008 (Mann-Whitney U-test, P<0.032). Annual differences in $\delta^{13}C_{FA}$ values could not be examined for ribbon seals due to sample size limitations.

Across all species comparisons of $\delta^{13}C_{FA}$ values of 11 FA showed that ringed, bearded, and spotted seals separated from each other in ordination space, and that spotted and ribbon seals did not (Fig. 3.8). Ringed, bearded, and spotted seals were significantly different in their $\delta^{13}C_{FA}$ profiles when analyzed as species across all years, seasons, and locations (PERMANOVA P=0.001). Bearded seals had higher $\delta^{13}C_{FA}$ values for all 11 FAs compared with ringed seals (Kruskal-Wallis ANOVA P<0.001, Fig. 3.9), and they had higher values than spotted seals for 7 of the 11 FAs (16:1n-7, 18:1n-11/9, 18:1n-7, 18:2n-6, 18:4n-3, 20:1n-11/9, 22:5n-3) (Kruskal-Wallis ANOVA P<0.001, Fig. 3.9). Spotted seals had higher $\delta^{13}C_{FA}$ values of 14:0, 16:0, 18:1n-11/9, 18:4n-3, 20:5n-3, 22:5n-3, and 22:6n-3 than ringed seals, although $\delta^{13}C_{FA}$ of 18:1n-7 was higher in ringed seals than in spotted seals (Kruskal-Wallis ANOVA P<0.022, Fig. 3.9). $\delta^{13}C_{FA}$ values for spotted and ribbon seals collected during spring-summer 2003 were not different (PERMANOVA P=0.773). The results from two stable isotope mixing models (one using 20:5n-

3, the other using 20:5n-3 and 22:6n-3) indicated that overall, bearded seals had the highest estimated contribution of i-POM in their diets (62 – 80%), followed by spotted seals (51 – 62%), then ringed seals (21 – 60%, Table 3.8). Concentration dependent model results were similar to results from models that did not use source concentrations for seals in 2009 using 20:5n-3, and for seals in 2010 using 20:5n-3 and 22:6n-3 as sources of i-POM (Table 3.8). Concentration dependent model results for seals in 2009 using 20:5n-3 and 22:6n-3 as sources of i-POM were slightly higher (between 7 – 10%) than the same model without concentration data (Table 3.8). In contrast, concentration dependent model results for bearded seals in 2010 using only 20:5n-3 as a source of i-POM were even greater (13%) than the results from the same model without concentration data (Table 3.8).

Discussion

Our results from the FA analysis corroborate previous findings that the diets of ringed, bearded, and spotted seals are different. They further show that diets remained constant over the years represented in this study, despite some variation of FA profiles within species. Our results are similar to those reported in Cooper et al. (2009) for ice seals sampled in 2003 from Little Diomede, Alaska, and indicate that the diet separation they found among bearded, ringed, and spotted seals remained similar in later years. Inferences about diet that we can make from our FA data also are similar to those made in Cooper et al. (2009). For example, shrimps (e.g., *Pandalus* spp.) apparently are still a main prey item for ringed seals as indicated by the lower proportions of 20:1n-9 and 22:1n-11 and higher proportions of 20:5n-3 and 22:6n-3 relative to the other ice seals (Iverson et al. 2002, Cooper et al. 2009). Bearded seals had higher total proportions of n-7 FA (16:1n-7, 18:1n-7, 20:1n-7), NMI FAs, and 20:4n-6 relative to the other ice seal species. The n-7 and NMI FAs indicate the importance of bivalves, such as clams (e.g., Budge et al. 2007, Cooper et al. 2009), and 20:4n-6 suggests sculpins (Cottidae) and shrimp (e.g., *Pandalus* spp.) in bearded seal diets (Iverson et al. 2002, Cooper et al. 2009), which corresponds with diets reported by Lowry et al. (1980a) and Dehn et al. (2007) from analysis of stomach contents and stable isotopes. Spotted and ribbon seal diets were similar, with both of them likely feeding on planktivorous fishes, based on high proportions of 20:1n-11, 20:1n-9, and 22:1n-11 in their blubber (Cooper et al. 2009). Although the proportions and species of prey cannot be determined from predator FA profiles and biomarkers alone, the predominance of NMI FAs in bearded seals compared with ringed, spotted, and ribbon seals is consistent with the more benthic prey found in the bearded seal diet (Lowry & Frost 1981, Dehn et al. 2007).

In this study, we were able to examine FA profiles for bearded seals sampled from Little Diomede in the Bering Sea and Point Hope in the Chukchi Sea for four years. Our results showed that diets of seals harvested near Little Diomede were different from seals sampled from Point Hope in 2005 and 2010, but not in 2007 and 2009. It is possible that the lack of difference between locations in 2007 (Little Diomede and Point Hope *n*=3) and 2009 (Little Diomede *n*=3, Point Hope *n*=4) could be due to insufficient samples sizes to detect statistical significance. In addition, these observations may not be due to geographic location but differences and similarities in Bering Sea spring sea ice extent in warm (2005) and cold years (2007, 2009, 2010). Bearded seals collected from Little Diomede and Point Hope are considered part of the Beringia population of bearded seals and most adults move south into the Bering Sea with the advancing ice edge in the winter and move northward in late spring, early summer to the Chukchi and Beaufort Seas (reviewed in Cameron et al. 2010). Furthermore, data from satellite tagged adult bearded seals suggest that seals enroute to the Chukchi and Beaufort seas in June are considered Bering Sea bearded seals that winter and breed in the Bering Sea (http://kotzebueira.org/environmental-projects/young-bearded-seal/index.html). Thus, if we assume that the differences in diets of bearded seals is not due to the geographic location then the variation in diet between 2005 and 2010 might be attributed to sea ice extent in a warm year (2005) compared to a cold year (2010) in the Bering Sea. Additionally, ice seals are highly mobile (Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010, Crawford et al. 2012), and seals sampled from one location could have been feeding in another location before they were harvested. However, the diet of bearded seals, and ice seals in general, can be highly variable (reviewed in Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010), likely due to the geographic differences in prey assemblages (Lowry et al. 1980b). Thus, linking differences in FA signatures and diet to differences in sampling locations should be done with caution.

Ringed and bearded seal FA profiles did not vary between the summer-spring and fall-winter months, indicating no change in diet, which is consistent with results from stomach content analysis of bearded seals harvested between 1960 – 2009 (Quakenbush et al. 2011b). In addition, Carroll et al. (2013) did not find a consistent seasonal pattern in the $\delta^{13}C$ and $\delta^{15}N$ values of ringed seal claws. In contrast, evidence from stomach content analysis of ringed seals harvested between 1960 – 2000 showed that fishes and amphipods were consumed more frequently in winter than summer by ringed seals, while mysids were consumed less frequently in winter than summer (Quakenbush et al. 2011a). This difference in results of our study and Carroll et al. (2013) compared with Quakenbush et al. (2011a) for ringed seals may be due to the different temporal scales that the analyses represent:

stomach content analysis provides information on recent feeding, while blubber FA profiles reflect an average of prey acquired over weeks to several months (Iverson et al. 2004, Nordstrom et al. 2008, Tollit et al. 2010), and stable isotopes from claw sheaths incorporate seasonal and interannual changes in diet, and can reflect dietary information for up to 10 years (McLaren 1958, Smith & Stirling 1975, Ferreira et al. 2011, Carroll et al. 2013). Thus, snapshots of the recent feeding from stomach analyses may have been more variable between seasons than the longer-term, seasonally integrated diet inferred from FA analysis. Annual variation in FA profiles was found inconsistently for ringed, bearded, and spotted seals. The FAs that explained those differences across years may stem from changes in the consumption and/or availability of certain prey. For example, the two FAs that consistently made the highest contribution to the annual variation in spotted seal FA profiles were 20:1n-11 and 22:1n-11. Changes in the proportions of these FAs could reflect differences in the types of planktivorous fishes and invertebrates that were consumed by spotted seals (Graeve et al. 1997, Budge et al. 2002, Iverson et al. 2002). Spotted seals rely on seasonally abundant fishes such as Pacific herring (*Clupea pallasii*), capelin, and smelt (Osmeridae) (Dehn et al. 2007, Boveng et al. 2009, Quakenbush et al. 2009). Therefore, changes in the seasonal abundance in planktivorous fishes may be reflected in the annual variation in FA profiles of spotted seals.

Ringed and bearded seal FA profiles (pooled by species) during the cold period in the Bering Sea did not change from those during the warm period, which suggests that their diets were not affected by these large multiyear environmental fluctuations. In contrast, most of the $\delta^{13}C_{FA}$ values found in bearded seals sampled in 2004 and 2005 were lower than those from bearded seals sampled in 2007 – 2010. The Bering Sea was relatively warm during 2001 – 2005 with low spring ice extent and warmer water column temperatures, but was relatively cold during 2007 – 2010 with extensive sea ice, cold water temperatures, and large spring ice-edge blooms (Stabeno et al. 2012a). These results suggest that the sources of FAs of bearded seal prey may have shifted from more pelagic sources in warm years (2004 and 2005, relatively lower $\delta^{13}C_{FA}$) to more sympagic sources in cold years (2007 – 2010, relatively higher $\delta^{13}C_{FA}$). This scenario assumes that bearded seals collected in the spring and summer were mainly feeding in the Bering Sea in the winter, and blubber FA profiles reflect dietary history for the previous winter and spring (see discussion below on blubber turnover rates). Ice seals are highly mobile and tend to migrate seasonally (Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010, Crawford et al. 2012). In the fall-winter months, bearded seals are found near the ice edge in the Bering Sea and follow the ice edge as it retreats northwards, spending the summers around the southern edge of the pack ice in the Chukchi and Beaufort Seas (reviewed in Cameron et al.

2010). Thus, it is reasonable to believe that their FA profiles reflect their dietary history from the previous winter in the Bering Sea. While extensive sea ice conditions in the Bering Sea would lead to higher $\delta^{13}C_{FA}$ values as described above, the opposite would be true during low sea ice conditions in the other part of their Arctic range during these same years (NSIDC 2011, Stabeno et al. 2012b). Furthermore, the Bering Sea recorded extensive spring sea ice from to 2007 – 2010, while extremely low minimum summer sea ice extent was recorded for those same years (2007 – 2010) in most Arctic seas, including the Chukchi and Beaufort Seas (NSIDC 2011, Stabeno et al. 2012b). Lower minimum Arctic summer sea ice extent would result in lower $\delta^{13}C_{FA}$ values in the Arctic compared with the cold years in the Bering Sea. Thus, an alternative but less likely explanation for the differences in $\delta^{13}C_{FA}$ values in bearded seals between those two time periods is that bearded seals in 2004 and 2005 foraged more in the Beaufort Sea in the winter, while seals in 2007 – 2010 foraged more in the Bering Sea.

Our isotope mixing model estimates indicated that a sympagic-based food web contributed to the diets of ringed, bearded, and spotted seals to varying degrees in 2009 and 2010. Despite the assumptions made while employing our models, some variability between results of the models, and some variability in the $\delta^{13}C_{FA}$ values within species, the data from all of our models illustrated that the strongest link with i-POM derived FAs was for bearded seals (62 – 79%), followed by spotted seals (51 – 62%), then ringed seals (21 – 60%). Although we did not estimate the proportional contribution of POM sources to seal species harvested from 2003 to 2008 (due to lack of POM data in those years), the $\delta^{13}C_{FA}$ data for ribbon seals collected in 2003 suggests that their degree of association with sea ice-derived FAs was similar to that of spotted seals. Ringed seals had the lowest association with sea-ice derived FAs, which was surprising, considering their reliance on ice-associated gadids, specifically Arctic cod (*Boreogadus saida*) (McLaren 1958, Lowry et al. 1980b, Dehn et al. 2007, Quakenbush et al. 2011a). The association with sea ice for Arctic cod includes shelter and protection from predators (Gradinger & Bluhm 2004) and sympagic amphipods for food (Lønne & Gulliksen 1989, Renaud et al. 2012). The relative contribution of ice algal FAs 16:4n-1 and 20:5n-3 to Arctic cod collected from Barrow and Cooper Island, Alaska in 2002 ranged between 8 to 77% (Budge et al. 2008). Thus, the lower association with sea ice-derived FAs could indicate that ringed seals in 2009 and 2010 were not consuming as much Arctic cod in those years, which is consistent with results from stable isotope analysis in Carroll et al. (2013). Alternatively, Graham et al. (2014) found that the proportional contribution of 16:4n-1, 20:5n-3, and 22:6n-3 from i-POM was ≤ 2% in juvenile Arctic cod collected from the Beaufort Sea between August and September 2011. Furthermore, demersal and pelagic Arctic cod from the

Beaufort Sea in 2008 had different diets: demersal cod fed more on fish while pelagic cod fed primarily on copepods and euphausiids (Rand et al. 2013). Consequently, consumption of Arctic cod and/or other fishes not associated with sea ice could explain the lower contribution of i-POM to ringed seals.

The wide range of estimates of sympagic FAs in the ice seal species analyzed could also be due to their mobility and the possibility that they could be foraging in different areas. Thus, the consumption of prey in different areas with varying $\delta^{13}C_{FA}$ values could also lead to differences in these estimates. For example, lower bulk $\delta^{13}C$ values for zooplankton from the Beaufort Sea (Schell et al. 1998) are thought to be the reason for lower bulk $\delta^{13}C$ muscle values in ringed seals and the wide range of $\delta^{13}C$ values in bearded seals because the Beaufort Sea is included in the range of both species (Dehn et al. 2007). The higher association with sea-ice derived FAs in spotted seals than in ringed seals in 2009 may be due to the timing and location of sampling. All but one of the spotted seals in 2009 were collected in September and October from Shishmaref in the southern Chukchi Sea, while ringed seals in 2009 were collected during fall-winter and spring summer months at locations south of Shishmaref (Little Diomede, Savoonga, and Hooper Bay) in the Bering Sea. A progressive decrease in bulk $\delta^{13}C$ values from west to east of marine benthic fauna and zooplankton from the southeast Bering Sea to the eastern Beaufort Sea has been identified (Dunton et al. 1989, Saupe et al. 1989). During August-October 1991-1994, Alaskan spotted seals were mostly nearshore in the Bering Sea, typically 200 km south of the ice edge in the Chukchi Sea (Lowry et al. 2000). In a recent study, satellite tagged adult ringed seals from Kotzebue Sound, Alaska made localized movements in the Chukchi and northern Bering seas and remained in those areas in the winter-spring season on shorefast or heavy pack ice to maintain breeding territories (Crawford et al. 2012). Thus, spotted seals were likely foraging in areas with higher $\delta^{13}C_{FA}$ values than ringed seals, which could also explain the higher estimates of sea-ice derived FAs in spotted seals relative to ringed seals in 2009.

Bearded seals had the greatest apparent incorporation of sea-ice derived FAs compared with ringed and spotted seals, which is likely due to their benthic feeding habits (France 1995, Dehn et al. 2007). Benthic organisms have higher $\delta^{13}C$ values than pelagic organisms (e.g., McConnaughey & McRoy 1979, Iken et al. 2010), and there are several explanations as to why this might be. One is that the relatively high $\delta^{13}C$ values are a result of benthic organisms consuming material that has undergone bacterial remineralization (McConnaughey & McRoy 1979). Alternatively, high $\delta^{13}C$ values in benthic organisms can also be a result of direct input of ice algae in shallow waters based on tight sympagic-benthic coupling in the Arctic (Sun et al. 2009). In addition, stagnant boundary

layers within low turbulence systems such as the sea floor may create a semi-closed system in which microphytobenthos might become more enriched in ^{13}C than pelagic phytoplankton (France 1995). Thus, the association of bearded seals with sea-ice derived FAs could not only reflect the amount of FAs from sea ice input to benthic organisms but also the processes by which benthic prey become more enriched in ^{13}C. Clearly these mechanisms of enrichment of Bering Sea and Arctic benthic organisms warrant further research and their $\delta^{13}C_{FA}$ values need to be characterized.

Our results differed from Budge et al. (2008), in that the contribution of sympagic FAs to ringed and bearded seals harvested in July 2002 during subsistence hunts in Barrow, Alaska, using the diatom FA marker 20:5n-3, was estimated to be lower (range for ringed seals: -5 – 12%, range for bearded seals: -25 – 23%) than our estimates, while their assessments using the diatom marker 16:4n-1 were comparable (range for ringed seals: 56 – 65%, range for bearded seals: 30 – 72%) to our study. These results from only the diatom FA marker 20:5n-3 suggest that ringed and bearded seals in Barrow acquired sympagic FAs to a lesser degree than seals from the Bering Sea. However, as already mentioned, ice seals are highly mobile, and seals collected in Barrow could have been foraging in an area with lower $\delta^{13}C_{FA}$ values, such as the Beaufort Sea (Schell et al. 1998). Feeding in areas with lower stable carbon isotope values would result in a lower estimated contribution of sea ice algae to ice seals as seen in ringed seals from Holman, Canada (lower $\delta^{13}C$ values from foraging in Beaufort Sea) compared with those from Barrow, Alaska (higher $\delta^{13}C$ values from foraging in the Chukchi Sea) (Dehn et al. 2007). Differences between this study and results from Budge et al. (2008) could also be due to several factors, such as different sources used in the model (i.e., pure ice algae and phytoplankton in Budge et al. (2008) vs. i-POM and p-POM in this study), as well as different sample locations and years. Furthermore, Budge et al. (2008) used a simple two-end mixing model, while in this study, we used a Bayesian multi-source stable isotope mixing model, which takes into account the uncertainty and variation of the i-POM and p-POM sources (Parnell et al. 2010). The $\delta^{13}C_{FA}$ value of 20:5n-3 of bearded seals from Budge et al. (2008) harvested in 2002 was -26.9 ‰, which is similar to values found for bearded seals in this study in 2009 (-26.7 ‰) and 2010 (-26.4 ‰). Therefore, the differences between results for bearded seals could be due to differences in FA sources and models used, but also from spatial or temporal variation. Bearded seals from Budge et al. (2008) were collected in July 2002 near Barrow, Alaska in the Chukchi-Beaufort Sea while bearded seals in 2009 and 2010 in this study were collected primarily from Point Hope and Little Diomede further south of Barrow. If all seals from both studies wintered in the Bering Sea, then the differences in estimates could be

attributed to differences in sources of the model. However, there is thought to be a small portion of Beringia bearded seals that winter and breed in the eastern Chukchi and Beaufort seas (Burns & Frost 1979). Thus, spatial variation may have also affected the model results. Additionally, as with any stable isotope study, there is the potential for input from as yet unmeasured isotopic sources that are unaccounted for (e.g., benthic algae, McTigue & Dunton 2014) that could also potentially explain the higher $\delta^{13}C_{FA}$ values in bearded seals and should be explored further.

Our estimates of sea-ice derived FAs to ice seals seem to be high when the contribution of sea ice algae to the total primary production is taken in consideration. In both the Bering and Chukchi Seas, annual production by water column phytoplankton in any year is likely much higher than production by sea ice phytoplankton. For instance, the proportion of the total primary production originating from sea ice algae in the Bering Sea has been estimated between as little as 3% and up to 30% (McRoy & Goering 1976, Gradinger unpublished data). Less is known about production dynamics on the Chukchi Sea shelf, but recent evidence suggests that water column primary production may be much higher than previously estimated (Arrigo et al. 2012, 2014). If the amount of sea ice algae that is available to consumers and transferred through the food web is a fraction of what is accessible from water column primary production, then how is it possible to have estimates for upper trophic level consumers that are as high as 50%, especially for species such as spotted seals that have a lower association with sea ice than the other seal species and also a generally pelagic diet? A plausible explanation could be associated with some of the assumptions made using the SIAR model. For example, mixing models often assume that the proportional contribution of a diet source to a consumer is the same for all components included (Phillips & Koch 2002), which in this case was FAs. However, the proportions of FAs often vary between prey and primary production sources, thus the estimates of the proportional contribution of sources could skew toward one source or another depending on their proportions. The proportions of 20:5n-3 in i-POM and p-POM in 2009 only differed by ~3%, while in 2010 the proportion of 20:5n-3 in i-POM was twice as much (20%) than in p-POM (10%). The model estimate for bearded seals in 2010 using only 20:5n-3 as a source without concentration data was higher (72%) than the estimate that incorporated concentration data (59%), which could explain the higher estimate for bearded seals in 2010. However, the estimates for ringed seals in 2010 using the same model parameters were not so different (without concentration data = 47%, with concentration data 43%). In addition to taking into account i-POM and p-POM FA concentration data, we assumed that the trophic enrichment factor (or fractionation) to be 0 (see discussion below) for 20:5n-3 and 22:6n-3. Fractionation of these two FAs from POM to seals would also influence the estimates of the model. For

instance, if the $\delta^{13}C_{FA}$ became heavier in the consumer relative to the source, estimates would be skewed toward the heavier source (i-POM). Further research is required to understand how the contribution of relatively small amounts of sea ice primary production compared with pelagic primary production is magnified in the food webs of ice seals.

The community composition of i-POM and p-POM used to estimate their relative contributions to consumers determines which FAs might give the most accurate mixing model estimates. In other words, if a POM sample is dominated by diatoms then using the diatom FA marker 20:5n-3 is likely the most appropriate. If non-diatom phytoplankton are present, such as flagellates, it might also be appropriate to include 22:6n-3. Some of the variability between the two model estimates is therefore likely derived from the different sources (i.e., diatom or flagellate) of the FAs used (Chapter 2). In addition to considering which FAs to use in estimating the contribution of i-POM to consumers, we assumed that the isotopic fractionation associated with the metabolism of FAs analyzed is negligible (Budge et al. 2008, 2011). Budge et al. (2011) found no isotopic discrimination of 20:5n-3 and 22:6n-3 between the diet and adipose tissue of two species of eiders (*Polysticta stelleri* and *Somateria fischeri*). Furthermore, Iverson et al. (2004) found very similar proportions of 20:5n-3 and 22:6n-3 in the blubber of juvenile gray (*Halichoerus grypus*) and harp seals (*Pagophilus groenlandicus*), and suckling gray seal pups and their prey, suggesting little modification from prey to predator. Therefore, if these FAs are incorporated from diet into blubber without modification, it is reasonable to assume that their $\delta^{13}C_{FA}$ values also remain unchanged. However, Rosen & Tollit (2012) found that this was not the case for Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and harbor seals (*Phoca vitulina richardsii*). Thus, even though we assumed little change in the $\delta^{13}C_{FA}$ of 20:5n-3 and 22:6n-3 due to modification in ice seals, further studies are warranted to confirm this.

In addition to assuming negligible isotopic discrimination, we assumed that lipid turnover in ice seals is instantaneous (Budge et al. 2008). At higher trophic levels, the lipids in i-POM and p-POM are not directly incorporated into ice seal blubber because POM lipids need to be consumed and assimilated at several lower trophic levels before being consumed by the seals. FAs in marine mammal blubber contain information about diet integrated over a period of weeks to months (Iverson et al. 2004, Nordstrom et al. 2008, Tollit et al. 2010), and changes in diet can be detected in blubber FAs in as little as one month (Iverson 2002). Ice seals sampled in the spring-summer (April – July) are pupping, nursing, and molting (Boveng et al. 2008, 2009, Cameron et al. 2010, Kelly et al. 2010); thus, animals are not feeding as much during spring-summer compared with the fall-winter months and the energy requirements are different between these two periods. The rate at which dietary FAs in ice seals are incorporated

into their blubber will determine if there was sufficient time to incorporate $\delta^{13}C_{FA}$ from i-POM and p-POM. In addition, selective mobilization of FAs of blubber to milk in lactating Weddell seals (*Leptonychotes weddelli*) affected the diet predictions when highly mobilized FAs were removed from the diet analysis (Wheatley et al. 2007). However, mobilization was not uniform within the blubber sample (i.e., inner versus outer layer), and full-thickness blubber core samples were suggested to be more reliable for making diet estimates during parturition (Wheatley et al. 2007). Additionally, changes in blubber FA composition observed following changes in diet appear to be greater than those occurring during fasting in Antarctic fur seals (*Arctocephalus gazelle*) and harp seals (Iverson et al. 1997b, Kirsch et al. 2000). Furthermore, a long-term fasting study on northern elephant seal pups (*Mirounga angustirostris*) showed no change in the overall FA profiles between weaning and 55 days post weaning (Noren et al. 2013). It is unknown whether the same is true for adult ice seals that are fasting and feeding at reduced levels. Fall-winter ringed seals were sampled in December 2009 and February 2010, and fall-winter spotted seals in 2009 were sampled in September and October 2009 likely reflect the diets of seals from several weeks to months previous (see above). During the fall and winter months, animals are actively feeding, putting on blubber (Ashwell-Erickson et al. 1979, Cameron et al. 2010, Kelly et al. 2010) and are presumably incorporating dietary FAs into blubber while actively feeding compared with the spring-summer months when feeding is limited. The duration that a $\delta^{13}C_{FA}$ signal from i-POM and p-POM persists in ice seal blubber is unknown, but it is clearly linked to the duration of that $\delta^{13}C_{FA}$ signal in their prey. Thus, turnover time can complicate interpretation of these data, and controlled feeding experiments with marine mammals as well as their prey are needed to better understand modification, mobilization, and turnover rates of dietary FAs in marine mammals.

The pairing of FA and $\delta^{13}C_{FA}$ data linked ice seal diets with sea ice biota within the marine food web. Our results support the idea that climate-induced changes to the amount of sympagic and pelagic organic matter input to the food web in the Bering Sea may affect the sources of primary productivity in the prey of ice seals. The timing of primary production is important to lower trophic level consumers such as zooplankton and any temporal offset with the timing of reproductive events may affect the diets of upper trophic level predators. If under-ice phytoplankton blooms seen in the Chukchi Sea (Arrigo et al. 2014) begin to increase, the ecosystem could potentially be flooded by water column primary production, and their associated lower $\delta^{13}C_{FA}$ values could also be transferred to the benthic food web, which then may reflect the higher amount of p-POM reaching the sea floor. The amount of water column primary production has already increased in areas of the Arctic and is also predicted to increase in the Bering Sea

(Brown & Arrigo 2012). As a result, more FAs from p-POM could be available to consumers. Although changes in diet are not necessarily negative, continued monitoring of ice seal diets and quantifying the proportional contribution of sea ice-derived organic matter to ice seals over time will help identify future changes in sea ice dynamics due to climate change and predict how these changes might affect their foraging ecologies.

Acknowledgements

This project was funded by the National Science Foundation (ARC-0902177 and 0732767). Financial support for S. Wang was also provided by the NSF, North Pacific Research Board Graduate Research Award, the University of Alaska Center for Global Change Student Research Grant with funds from the Cooperative Institute for Alaska Research, Robert Byrd Award, Dieter Family Marine Science Research Scholarship, and the Ken Turner Memorial Fellowship. The seal harvest sampling was primarily funded by the NOAA Fisheries, Alaska Region under award NA11NMF4390200 with partial funding by the North Pacific Research Board to the Alaska Department of Fish and Game. We are indebted to the residents of Little Diomede, Gambell, Hooper Bay, Kivalina, Nome, Point Hope, Savoonga, and Shishmaref for providing samples from their subsistence hunts for this study. Thanks to A. Bryan (ADFG), H. Isernhagen (ADFG), A. Brenner (ADFG), and L. Oxtoby (UAF) for assistance with blubber sub-sampling. We also thank T. Howe (UAF), N. Haubenstock (UAF), C. Graham (UAF), and A. Timmins (Dalhousie) for support with laboratory analysis. We are grateful to A. Blanchard (UAF) for advice on statistical analyses. Finally, we thank K. Iken, A. Bryan, and L. Oxtoby for helpful discussions and constructive comments that improved the manuscript. Author Contributions: SWW wrote the manuscript. SWW performed the compound-specific stable isotope analysis and analyzed the data. MJW and SMB formulated the concept. SMB developed methodology and performed the fatty acid laboratory analysis. LHD, LTQ, and AMS provided editorial advice. LTQ provided the ice seal blubber samples.

References

ACIA (2004) Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, New York

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32-46

Antonelis G, Melin S, Bukhtiyarov Y (1994) Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74-79

Arrigo KR, Mock T, Lizotte MP (2010) Primary producers and sea ice. In: Thomas DN, Dieckmann GS (eds) Sea Ice. Wiley-Blackwell Oxford, United Kingdom

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bahr F, Bates NR, Benitez-Nelson C, Bowler B, Brownlee E, Ehn JK, Frey KE, Garley R, Laney SR, Lubelczyk L, Mathis J, Matsuoka A, Mitchell BG, Moore GWK, Ortega-Retuerta E, Pal S, Polashenski CM, Reynolds RA, Schieber B, Sosik HM, Stephens M, Swift JH (2012) Massive phytoplankton blooms under Arctic sea ice. Science 336:1408

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bates NR, Benitez-Nelson CR, Brownlee E, Frey KE, Laney SR, Mathis J, Matsuoka A, Greg Mitchell B, Moore GWK, Reynolds RA, Sosik HM, Swift JH (2014) Phytoplankton blooms beneath the sea ice in the Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 105:1-16

Ashwell-Erickson S, Elsner R, Wartzok D (1979) Metabolism and nutrition of Bering Sea harbor and spotted seals. In: Melteff BR (ed) Proceedings of the 29th Alaska Science Conference Alaska Fisheries: 200 Years and 200 Miles of Change Sea Grant Report 79-6. Alaska Sea Grant, Fairbanks, Alaska

Beck CA, Rea LD, Iverson SJ, Kennish JM, Pitcher KW, Fadely BS (2007) Blubber fatty acid profiles reveal regional, seasonal, age-class and sex differences in the diet of young Steller sea lions in Alaska. Marine Ecology Progress Series 338:269-280

Benjaminsen T (1973) Age determination and the growth and age distribution from cementum growth layers of bearded seals of Svalbard. Fiskeridir Skr Ser HavUnders 16:159-170

Bluhm BA, Gradinger R (2008) Regional variability in food availability for arctic marine mammals. Ecological Applications 18:S77-S96

Boveng PL, Bengtson JL, Buckley TW, Cameron MF, Dahle SP, Kelly BP, Megrey BA, Overland JE, Williamson NJ (2009) Status review of the spotted seal (*Phoca largha*). National Oceanic and Atmospheric Administration Technical Memorandum. NMFS-AFSC-200. U.S. Department of Commerce

Boveng PL, Bengtson JL, Buckley TW, Cameron MF, Dahle SP, Megrey BA, Overland JE, Williamson NJ (2008) Status review of the ribbon seal (*Histriophoca fasciata*). National Oceanic and Atmospheric Admistration Technical Memorandum. NMFS-AFSC-191. U.S. Department of Commerce

Brown ZW, Arrigo KR (2012) Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES Journal of Marine Science: Journal du Conseil 69:1180-1193

Bryan AL (2014) Identifying bearded and ringed seal diet - A comparison of stomach contents, stable isotopes, fatty acids, and fecal DNA. MS thesis, University of Alaska Fairbanks

Budge SM, Iverson SJ, Bowen WD, Ackman RG (2002) Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 59:886

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Marine Mammal Science 22:759-801

Budge SM, Springer AM, Iverson SJ, Sheffield G (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. Marine Ecology Progress Series 336:305-309

Budge SM, Wang SW, Hollmén TE, Wooller MJ (2011) Carbon isotopic fractionation in eider adipose tissue varies with fatty acid structure: implications for trophic studies. Journal of Experimental Biology 214:3790-3800

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117-129

Bukhtiyarov Y, Frost KJ, Lowry LF (1984) New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring. In: Fay FH, Fedoseev GA (eds) Soviet-American cooperative research on marine mammals Volume 1 - Pinnipeds Under Project V6 Marine Mammals, of the US-USSR Agreement on Cooperation in the Field of Enviromental Protection. U.S. Department of Commerce, NOAA Techincal Report NMFS 12, Washington, D. C.

Burns JJ (1971) Biology of the ribbon seal, *Histriophoca fasciata*, in the Bering Sea (Abstract). Proceedings of the Twenty-second Alaska Science Conference. Alaska Division of the American Association for the Advancement of Science, College, AK

Burns JJ (2002) Harbor seal and spotted seal, *Phoca vitulina* and *P. largha*. In: Perrin WF, Würsig B, Thewissen HGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, CA

Burns JJ, Frost KJ (1979) The natural history and ecology of the bearded seal, *Erignathus barbatus*. Alaska Department of Fish and Game. 77 p

Burns JJ, Shapiro LH, Fay FH (1981) Ice as marine mammal habitat in the Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle

Cameron MF, Bengtson JL, Boveng PL, Jansen JK, Kelly BP, Dahle SP, Logerwell EA, Overland JE, Sabine CL, Waring GT, Wilder JM (2010) Status review of the bearded seal (*Erignathus barbatus*). Book National Oceanic and Atmospheric Admistration Technical Memorandum. NMFS-AFSC-211. U.S. Department of Commerce

Carroll SS, Horstmann-Dehn L, Norcross BL (2013) Diet history of ice seals using stable isotope ratios in claw growth bands. Canadian Journal of Zoology 91:191-202

Clarke KR, Gorley RN (2006) PRIMER, version 6: user manual/tutorial, PRIME-E, Plymouth, UK

Clarke KR, Warwick RM (2001) Changes in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Cooper MH (2004) Fatty acid metabolism in marine carnivores: implications for quantitative estimation of predator diets. PhD Thesis, Dalhousie University, Halifax, NS

Cooper MH, Budge SM, Springer AM, Sheffield G (2009) Resource partitioning by sympatric pagophilic seals in Alaska: monitoring effects of climate variation with fatty acids. Polar Biology 32:1137-1145

Crawford JA, Frost KJ, Quakenbush LT, Whiting A (2012) Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. Polar Biology 35:241-255

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, Book 46. Academic Press

Dehn L-A, Sheffield G, Follmann E, Duffy L, Thomas D, O'Hara T (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biology 30:167-181

Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopc gradients among arctic and subarctic marine fauna. Marine Ecology Progress Series 56:89-97

Fay FH (1974) The role of ice in the ecology of marine mammals in the Bering Sea. In: Hood DW, Kelley EJ (eds) Oceanography of the Bering Sea. Institute of Marine Science, University of Alaska, Fairbanks

Ferreira EO, Loseto LL, Ferguson SH (2011) Assessment of claw growth-layer groups from ringed seals (*Pusa hispida*) as biomonitors of inter- and intra-annual Hg, $\delta^{15}N$, and $\delta^{13}C$ variation. Canadian Journal of Zoology 89:774-784

Finley KJ, Evans CR (1983) Summer diet of the bearded seal (*Erignathus barbatus*) in the Canadian High Arctic. Arctic 36:82-89

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry 226:497-509

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124:307-312

Frost KJ, Lowry LF (1980) Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Canadian Journal of Zoology 58:1601-1607

Gradinger RR (2002) Sea ice microorganisms. In: Bitten G (ed) Encyclopedia of environmental microbiology. Wiley and Sons, Hoboken, New Jersey, USA

Gradinger RR, Bluhm BA (2004) In-situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. Polar Biology 27:595-603

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biology 18:53-61

Graham C, Oxtoby L, Wang S, Budge S, Wooller M (2014) Sourcing fatty acids to juvenile polar cod (*Boreogadus saida*) in the Beaufort Sea using compound-specific stable carbon isotope analyses. Polar Biology 37:697-705

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annual Review of Marine Science 4:63-78

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Horner RA (1985) Taxonomy of sea ice microalgae. In: Horner RA (ed) Sea Ice Biota. CRC Press, Boca Raton, Florida, USA

Hunt GL, Jr., Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Research Part II: Topical Studies In Oceanography 49:5821-5853

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Research Part II: Topical Studies In Oceanography 57:71-85

Iverson SJ (2002) Blubber. In: Perrin WF, Wursig B, Thewissen HGM (eds) Encyclopedia of marine mammals. Academic Press, San Diego

Iverson SJ, Arnould JPY, Boyd IL (1997b) Milk fatty acid signatures indicate both major and minor shifts in the diet of lactating Antarctic fur seals. Canadian Journal of Zoology 75:188-197

Iverson SJ, Field C, Bowen WD, Blanchard W (2004) Quantitative fatty acid signature analysis: A new method of estimating predator diets. Ecological Monographs 74:211-235

Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Marine Ecology Progress Series 241:161-181

Iverson SJ, Frost KJ, Lowry LF (1997a) Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Marine Ecology Progress Series 151:255-271

Kelly BP (1988) Ribbon seal, *Phoca fasciata*. In: Lentfer JW (ed) Selected Marine Mammal Species of Alaska: Species Accounts with Research and Management Recommendations. Marine Mammal Commission, Washington, D.C.

Kelly BP, Bengtson JL, Boveng PL, Cameron MF, Dahle SP, Jansen JK, Logerwell EA, Overland JE, Sabine CL, Waring GT, Wilder JM (2010) Status review of the Ringed Seal (*Phoca hispida*). Book National Oceanic and Atmospheric Admistration Technical Memorandum. NMFS-AFSC-212. U. S. Department of Commerce

Kirsch PE, Iverson SJ, Bowen WD (2000) Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). Physiological and Biochemical Zoology 73:45-59

Koopman HN, Iverson SJ, Gaskin DE (1996) Stratification and age-related differences in blubber fatty acids of the male harbour porpoise (*Phocoena phocoena*). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 165:628-639

Kotzebue Sound Bearded Seal Satellite Tagging Project. Native Village of Kotzebue. Kotzebue IRA. http://kotzebueira.org/environmental-projects/young-bearded-seal/index.html. Accessed July 22, 2014.

Lambert A, Meynier L, Donaldson L, Roe W, Morel PH (2013) Body regional distribution and stratification of fatty acids in the blubber of New Zealand sea lions: implications for diet predictions. Journal of Comparative Physiology B 183:145-156

Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Progress In Oceanography 90:18-32

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biology 9:187-191

Lowry LF (1985) The ribbon seal (*Phoca fasciata*). In: Burns JJ, Frost KJ, Lowry LF (eds) Marine Mammal Species Accounts. Alaska Department of Fish and Game, Juneau, AK

Lowry LF, Frost KJ (1981) Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle

Lowry LF, Frost KJ, Burns JJ (1980a) Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Canadian Journal of Fisheries and Aquatic Sciences 37:2254-2261

Lowry LF, Frost KJ, Burns JJ (1980b) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330-342

Lowry LF, Burkanov VN, Frost KJ, Simpkins MA, Davis R, DeMaster DP, Suydam R, Springer A (2000) Habitat use and habitat selection by spotted seals (*Phoca largha*) in the Bering Sea. Canadian Journal of Zoology 78:1959-1971

Mansfield AW, Fisher HD (1960) Age determination in the harbour seal, *Phoca vitulina* L. Nature 186:92-93

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290-297

McConnaughey T, McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology 53:257-262

McLaren IA (1958) The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctc. Bulletin Fisheries Research Board Canada 118:1-97

McRoy CP, Goering JJ (1976) Annual budget of primary production in the Bering Sea. Marine Science Communications 2:255-267

McTigue ND, Dunton KH (2014) Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 102:84-96

Moran SB, Lomas MW, Kelly RP, Gradinger R, Iken K, Mathis JT (2012) Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea. Deep Sea Research Part II: Topical Studies In Oceanography 65–70:84-97

NMFS (2012a) Endangered and threatened species; threatened status for Beringia and Okhost Distinct Population Segments of the *Erignathus barbatus nauticus* subspecies of the bearded seal; Final Rule. 77:76740-76768

NMFS (2012b) Endangered and threatened species; threatened ttatus for the Arctic, Okhotsk, and Baltic Subspecies of the ringed real and endangered status for the Ladoga subspecies of the ringed seal; Final Rule. 77:76706-76738

Nordstrom CA, Wilson LJ, Iverson SJ, Tollit DJ (2008) Evaluating quantitative fatty acid signature analysis (QFASA) using harbour seals *Phoca vitulina richardsi* in captive feeding studies. Marine Ecology Progress Series 360:245-263

Noren DP, Budge SM, Iverson SJ, Goebel ME, Costa DP, Williams TM (2013) Characterization of blubber fatty acid signatures in northern elephant seals (*Mirounga angustirostris*) over the postweaning fast. Journal of Comparative Physiology B 183:1065-1074

NSIDC (2011) Summer 2011: Arctic sea ice near record lows. http://nsidcorg/arcticseaicenews/2011/10/summer-2011-arctic-sea-ice-near-record-lows/. Accessed 9 May 2014

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672

Parrish CC (1999) Determination of total lipid, lipid classes and fatty acids in aquatic samples. In: Arts MT, Wainman BC (eds) Lipids in Freshwater Ecosystems. Springer-Verlag, New York

Perovich D, Gerland S, Hendricks S, Meier W, Nicolaus M, Richter-Menge J, Tschudi M (2013) Sea Ice [in Arctic Report Card 2013], http://www.arctic.noaa.gov/reportcard.

Phillips DL, Koch PL (2002) Incorporating concentration dependence in stable isotope mixing models. Oecologia 130:114-125

Quakenbush L, Citta J, Crawford J (2009) Biology of the Spotted Seal (*Phoca largha*) in Alaska from 1962 to 2008. Preliminary Report to National Marine Fisheries Service. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK

Quakenbush L, Citta J, Crawford J (2011a) Biology of the Ringed Seal (*Phoca hispida*) in Alaska from 1960-2010. Final Report to National Marine Fisheries Service. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK

Quakenbush L, Citta J, Crawford J (2011b) Biology of the bearded seal (*Erignathus barbatus*) in Alaska, 1962‐2009. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Final Report to National Marine Fisheries Service

Rand KM, Whitehouse A, Logerwell EA, Ahgeak E, Hibpshman R, Parker-Stetter S (2013) The diets of polar cod (*Boreogadus saida*) from August 2008 in the US Beaufort Sea. Polar Biology 36:907-912

Renaud PE, Berge J, Varpe Ø, Lønne OJ, Nahrgang J, Ottesen C, Hallanger I (2012) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biology 35:401-412

Rosen D, Tollit D (2012) Effects of phylogeny and prey type on fatty acid calibration coefficients in three pinniped species: implications for the QFASA dietary quantification technique. Marine Ecology Progress Series 467:263-276

Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope gradients in western arctic zooplankton. Marine Biology 103:427-432

Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Marine Ecology Progress Series 162:11-23

Simpkins MA, Hiruki-Raring LM, Sheffield G, Grebmeier JM, Bengtson JL (2003) Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. Polar Biology 26:577-586

Smith TG, Stirling I (1975) The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology 53:1297-1305

Søreide JE, Carroll ML, Hop H, Ambrose WG, Hegseth EN, Falk-Petersen S (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Marine Biology Research 9:831-850

Spindler M (1994) Notes on the biology of sea ice in the Arctic and Antarctic. Polar Biology 14:319-324

Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the south-eastern Bering Sea. Fisheries Oceanography 10:81-98

Stabeno PJ, Bond NA, Salo SA (2007) On the recent warming of the southeastern Bering Sea shelf. Deep Sea Research Part II: Topical Studies In Oceanography 54:2599-2618

Stabeno PJ, Farley Jr EV, Kachel NB, Moore S, Mordy CW, Napp JM, Overland JE, Pinchuk AI, Sigler MF (2012b) A comparison of the physics of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem. Deep Sea Research Part II: Topical Studies In Oceanography 65–70:14-30

Stabeno PJ, Hunt Jr GL (2002) Overview of the Inner Front and Southeast Bering Sea Carrying Capacity Programs. Deep Sea Research Part II: Topical Studies in Oceanography 49:6157-6168

Stabeno PJ, Kachel NB, Moore SE, Napp JM, Sigler M, Yamaguchi A, Zerbini AN (2012a) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Research Part II: Topical Studies In Oceanography 65–70:31-45

StatSoft, Inc (2013) STATISTICA (Data Analysis Software System), version 12. www.statsoft.com.

Stewart REA, Steward BE, Stirling I, Street E (1996) Counts of growth layer groups in cememtum and dentine in ringed seals (*Phoca hispida*). Marine Mammal Science 12:383-401

Sun M-Y, Clough LM, Carroll ML, Dai J, Ambrose Jr WG, Lopez GR (2009) Different responses of two common Arctic macrobenthic species (*Macoma balthica* and *Monoporeia affinis*) to phytoplankton and ice algae: Will climate change impacts be species specific? Journal of Experimental Marine Biology and Ecology 376:110-121

Thiemann GW, Iverson SJ, Stirling I (2007) Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. Marine Mammal Science 23:241-261

Thiemann GW, Iverson SJ, Stirling I (2008) Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic. Marine Mammal Science 24:91-111

Tollit DJ, Pierce GJ, Hobson KA, Bowen WD, Iverson SJ (2010) Diet. In: Boyd IL, Bowen WD, Iverson SJ (eds) Marine mammal ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom

Viso A-C, Marty J-C (1993) Fatty acids from 28 marine microalgae. Phytochemistry 34:1521-1533

Walton M, Pomeroy P (2003) Use of blubber fatty acid profiles to detect inter-annual variations in the diet of grey seals *Halichoerus grypus*. Marine Ecology Progress Series 248:257-266

Walton MJ, Henderson RJ, Pomeroy PP (2000) Use of blubber fatty acid profiles to distinguish dietary differences between grey seals *Halichoerus grypus* from two UK breeding colonies. Marine Ecology Progress Series 193:201-208

Wang M, Overland JE (2009) A sea ice free summer Arctic within 30 years? Geophysical Research Letters 36:L07502

Wang M, Overland JE (2012) A sea ice free summer Arctic within 30 years: An update from CMIP5 models. Geophys Res Lett 39:L18501

Wang SW, Budge SM, Gradinger RR, Iken K, Wooller MJ (2014) Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia 174:699-712

Wheatley KE, Nichols PD, Hindell MA, Harcourt RG, Bradshaw CJA (2007) Temporal variation in the vertical stratification of blubber fatty acids alters diet predictions for lactating Weddell seals. Journal of Experimental Marine Biology and Ecology 352:103-113

Ziel HL, Cameron MF, Boveng PL (2008) Spring diet of ribbon and spotted seals in the Bering Sea (Poster presentation). In: Alaska Fisheries Science Center NMFS, NOAA (ed), Seattle, WA

Table 3.1. Samples sizes for full-thickness blubber collected from adult ringed, bearded, spotted, and ribbon seals by year and season. All samples were analyzed for fatty acids. Numbers in parentheses are the sample sizes used in the $\delta^{13}C_{FA}$ analysis

Year	Season	Ringed Seal	Bearded Seal	Spotted Seal	Ribbon Seal
2002	Spring-Summer	0	7	0	0
	Fall-Winter	0	0	0	0
2003	Spring-Summer	1	6	9 (2)	15 (5)
	Fall-Winter	5	0	1	0
2004	Spring-Summer	1	7	1	0
	Fall-Winter	0	2	2	0
2005	Spring-Summer	2	25 (23)	0	0
	Fall-Winter	3	0	3	0
2006	Spring-Summer	1	6 (5)	2	0
	Fall-Winter	3 (2)	0	1	0
2007	Spring-Summer	2	8	0	0
	Fall-Winter	3	0	7	0
2008	Spring-Summer	2	11 (10)	0	1
	Fall-Winter	10	0	14	0
2009	Spring-Summer	7	10	0	0
	Fall-Winter	8	0	11	0
2010	Spring-Summer	3	20	0	0
	Fall-Winter	0	0	0	0
Total		51 (50)	102 (99)	51 (44)	16 (6)

Table 3.2. PERMANOVA analysis results of adult ringed and bearded seal fatty acid profiles between spring-summer and fall-winter months. Permutations = number of unique permutations

Ringed Seal			Bearded Seal		
Years	*P*	Permutations	Years	*P*	Permutations
2005	*0.499*	10	2004	*0.357*	36
2007	*0.601*	10			
2008	*0.338*	66			
2009	*0.311*	910			

Table 3.3. PERMANOVA analysis results of adult ringed, bearded, and spotted seal fatty acid profiles among years. *P* values for pairwise comparisons, values in **bold** type indicate significance at $\alpha<0.05$. n/a indicates that the comparison between years could not be made. Data were pooled across all months for ringed and bearded seals. For spotted seals, the annual comparisons were made for the fall-winter months only. Permutations = number of unique permutations

	Ringed Seal Overall *P=0.009* Permutations=998		Bearded Seal Overall *P=0.025* Permutations=998		Spotted Seal Overall *P=0.012* Permutations=998	
Year	*P*	Permutations	*P*	Permutations	*P*	Permutations
2002-2003	*n/a*	*n/a*	*0.094*	921	*n/a*	*n/a*
2002-2004	*n/a*	*n/a*	*0.140*	960	*n/a*	*n/a*
2002-2005	*n/a*	*n/a*	*0.087*	999	*n/a*	*n/a*
2002-2006	*n/a*	*n/a*	***0.039***	756	*n/a*	*n/a*
2002-2007	*n/a*	*n/a*	*0.243*	737	*n/a*	*n/a*
2002-2008	*n/a*	*n/a*	*0.057*	975	*n/a*	*n/a*
2002-2009	*n/a*	*n/a*	***0.038***	968	*n/a*	*n/a*
2002-2010	*n/a*	*n/a*	***0.011***	997	*n/a*	*n/a*
2003-2004	*n/a*	*n/a*	*0.169*	761	*n/a*	*n/a*
2003-2005	*0.166*	408	*0.062*	998	*n/a*	*n/a*
2003-2006	*0.083*	208	*0.091*	763	*n/a*	*n/a*
2003-2007	*0.444*	398	*0.059*	763	*n/a*	*n/a*
2003-2008	*0.371*	977	*0.077*	965	*n/a*	*n/a*
2003-2009	*0.423*	992	*0.070*	940	*n/a*	*n/a*
2003-2010	*0.074*	84	***0.004***	992	*n/a*	*n/a*
2004-2005	*n/a*	*n/a*	*0.646*	997	*0.330*	10
2004-2006	*n/a*	*n/a*	*0.200*	919	*n/a*	*n/a*
2004-2007	*n/a*	*n/a*	*0.561*	959	***0.044***	120
2004-2008	*n/a*	*n/a*	*0.502*	996	***0.035***	516
2004-2009	*n/a*	*n/a*	*0.219*	993	***0.007***	341
2004-2010	*n/a*	*n/a*	*0.196*	997	*n/a*	*n/a*
2005-2006	*0.192*	126	*0.178*	999	*n/a*	*n/a*
2005-2007	*0.239*	126	*0.686*	999	*0.204*	120
2005-2008	*0.424*	926	*0.768*	999	*0.423*	527
2005-2009	*0.266*	969	*0.203*	998	*0.624*	333
2005-2010	***0.045***	56	*0.772*	999	*n/a*	*n/a*
2006-2007	***0.005***	126	***0.037***	781	*n/a*	*n/a*
2006-2008	***0.024***	759	*0.228*	961	*n/a*	*n/a*
2006-2009	***0.038***	865	*0.759*	937	*n/a*	*n/a*
2006-2010	*0.976*	35	*0.052*	998	*n/a*	*n/a*
2007-2008	*0.856*	917	*0.313*	992	*0.431*	994
2007-2009	*0.541*	960	*0.089*	967	***0.001***	981
2007-2010	***0.020***	56	*0.250*	999	*n/a*	*n/a*
2008-2009	*0.691*	998	*0.546*	997	***0.010***	999
2008-2010	***0.015***	416	*0.313*	999	*n/a*	*n/a*
2009-2010	***0.013***	563	*0.051*	998	*n/a*	*n/a*

Table 3.4. PERMANOVA analysis results of adult bearded seal fatty acid profiles between Little Diomede and Point Hope in 2005, 2006, 2009, and 2010. Values in **bold** type indicate significance at α <0.05. Permutations = number of unique permutations

Year	*P*	Permutations
2005	***0.005***	998
2007	*0.127*	10
2009	*0.122*	126
2010	***0.006***	674

Table 3.5. *P* values for the results from (a) Mann-Whitney U-test comparing each non-methylene interrupted (NMI) fatty acids (FAs) from Bering Sea warm and cold years for adult ringed and bearded seals and (b) Kruskal-Wallis ANOVA with multiple comparisons of NMI FAs among adult ringed, bearded, spotted, and ribbon seals. Values in **bold** type indicate significance at $\alpha < 0.05$

(a)

NMI FA	Ringed Seal	Bearded Seal
20:2Δ5,11	***0.013***	***0.016***
20:2Δ5,13	*0.405*	*0.997*
20:3Δ5,11,14	*0.857*	*0.138*
22:2NMID	*0.282*	*0.850*
22:2Δ7,13	*0.691*	*0.638*
22:2Δ7,15	*0.895*	*0.601*

(b)

20:2Δ5,11	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	***0.001***		
Spotted seal	*0.130*	***0.037***	
Ribbon seal	*1.000*	***0.013***	*1.000*

20:2Δ5,13	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	*1.000*		
Spotted seal	*1.000*	*0.891*	
Ribbon seal	***0.001***	***0.001***	***0.001***

20:3Δ5,11,14	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	***0.001***		
Spotted seal	*1.000*	***0.001***	
Ribbon seal	*0.321*	***0.001***	*0.260*

22:2NMID	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	***0.001***		
Spotted seal	*0.282*	***0.001***	
Ribbon seal	*0.260*	***0.001***	*1.000*

22:2Δ7,13	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	***0.001***		
Spotted seal	*1.000*	***0.001***	
Ribbon seal	*1.000*	***0.001***	*1.000*

22:2Δ7,15	Ringed Seal	Bearded Seal	Spotted Seal
Bearded seal	***0.001***		
Spotted seal	***0.002***	***0.001***	
Ribbon seal	*1.000*	***0.001***	*0.140*

Table 3.6. PERMANOVA analysis results for bearded and spotted seal $\delta^{13}C_{FA}$ values among years. *P* values for pairwise comparisons, values in **bold** type indicate significance at α <*0.05*. n/a indicates that the comparison between years could not be made. Data were pooled across all months for bearded seals. For spotted seals, the annual comparisons were made for the fall-winter months only. Permutations = number of unique permutations

	Bearded Seal Overall *P=0.001* Permutations=997		Spotted Seal Overall *P=0.025* Permutations=999	
Years	*P*	Permutations	*P*	Permutations
2004-2005	***0.007***	998	*0.090*	10
2004-2006	***0.008***	793	*n/a*	*n/a*
2004-2007	***0.004***	983	*0.144*	36
2004-2008	***0.001***	997	*0.064*	120
2004-2009	***0.001***	991	*0.055*	78
2004-2010	***0.001***	999	*n/a*	*n/a*
2005-2006	*0.798*	990	*n/a*	*n/a*
2005-2007	***0.002***	999	*0.166*	120
2005-2008	***0.001***	**999**	***0.028***	517
2005-2009	***0.001***	999	*0.200*	337
2005-2010	***0.001***	998	*n/a*	*n/a*
2006-2007	***0.018***	694	*n/a*	*n/a*
2006-2008	***0.002***	857	*n/a*	*n/a*
2006-2009	***0.004***	884	*n/a*	*n/a*
2006-2010	***0.002***	989	*n/a*	*n/a*
2007-2008	*0.745*	987	*0.433*	995
2007-2009	*0.931*	989	*0.246*	982
2007-2010	*0.631*	999	*n/a*	*n/a*
2008-2009	*0.493*	993	*0.176*	999
2008-2010	*0.192*	999	*n/a*	*n/a*
2009-2010	*0.633*	999	*n/a*	*n/a*

Table 3.7 Percentages of 20:5n-3 and 22:6n-3 in i-POM and p-POM from 2009 and 2010. Values were used as concentration dependencies in the SIAR stable isotope mixing models using diatom marker 20:5n-3 and flagellate marker 22:6n-3 as sources. Mean ± 1 SD

	20:5n-3		22:6n-3	
Source	Mean	SD	Mean	SD
i-POM 2009	20.3	7.6	2.2	0.8
p-POM 2009	23.2	4.4	3.8	0.5
i-POM 2010	19.6	6.6	2.5	0.8
p-POM 2010	10.3	5.8	5.0	3.7

Table 3.8. Estimates of i-POM (%) contribution to adult ringed, bearded, and spotted seals during spring-summer (SS) and fall-winter (FW) in 2009 and 2010 from SIAR stable isotope mixing models. Models used diatom marker 20:5n-3 and both 20:5n-3 and flagellate marker 22:6n-3 as sources of i-POM. Results shown for models that assumed no concentration dependency and concentration dependencies from Table 3.7. Sample sizes are given in Table 3.1. **Mean** ± 95% credibility interval

2009	Concentration Dependency=0			Concentration Dependency Included		
20:5n-3	**Mean**	Low 95% CI	High 95% CI	**Mean**	Low 95% CI	High 95% CI
Bearded Seal SS	**62**	41	87	**64**	44	88
Ringed Seal FW	**24**	2	47	**26**	3	50
Ringed Seal SS	**21**	0	50	**22**	0	51
Spotted Seal FW	**51**	32	72	**54**	35	74

2009	Concentration Dependency=0			Concentration Dependency Included		
20:5n-3, 22:6n-3	**Mean**	Low 95% CI	High 95% CI	**Mean**	Low 95% CI	High 95% CI
Bearded Seal SS	**80**	62	99	**87**	71	101
Ringed Seal FW	**42**	25	59	**50**	26	69
Ringed Seal SS	**39**	16	60	**46**	16	71
Spotted Seal FW	**62**	47	77	**72**	56	87

2010	Concentration Dependency=0			Concentration Dependency Included		
20:5n-3	**Mean**	Low 95% CI	High 95% CI	**Mean**	Low 95% CI	High 95% CI
Bearded Seal SS	**72**	54	91	**59**	40	82
Ringed Seal SS	**47**	6	85	**43**	3	83

2010	Concentration Dependency=0			Concentration Dependency Included		
20:5n-3, 22:6n-3	**Mean**	Low 95% CI	High 95% CI	**Mean**	Low 95% CI	High 95% CI
Bearded Seal SS	**61**	30	98	**62**	32	97
Ringed Seal SS	**60**	47	74	**60**	46	75

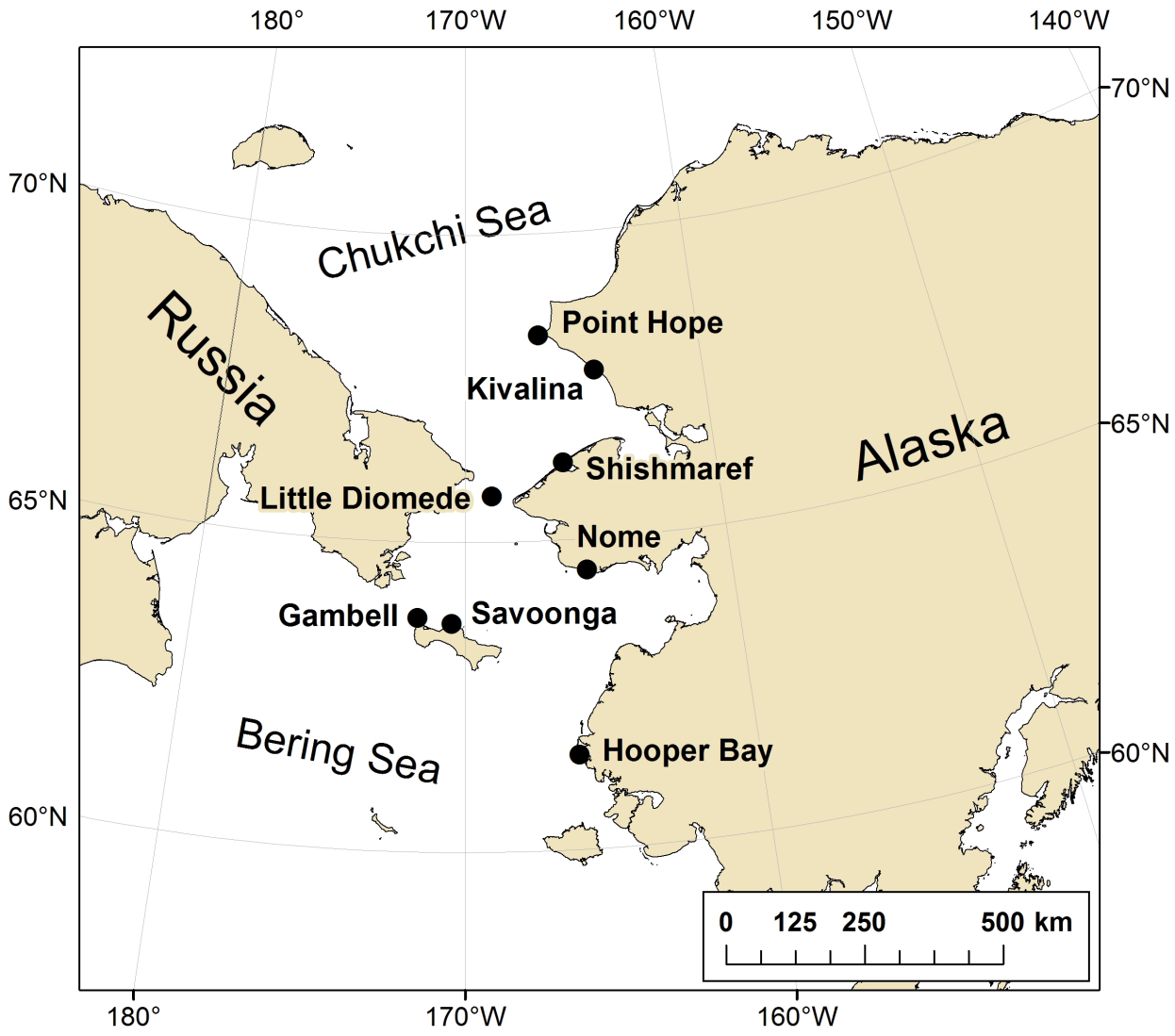


Figure 3.1. Map showing the locations of Alaska Native subsistence communities where blubber samples of adult ringed, bearded, spotted, and ribbon seals were collected

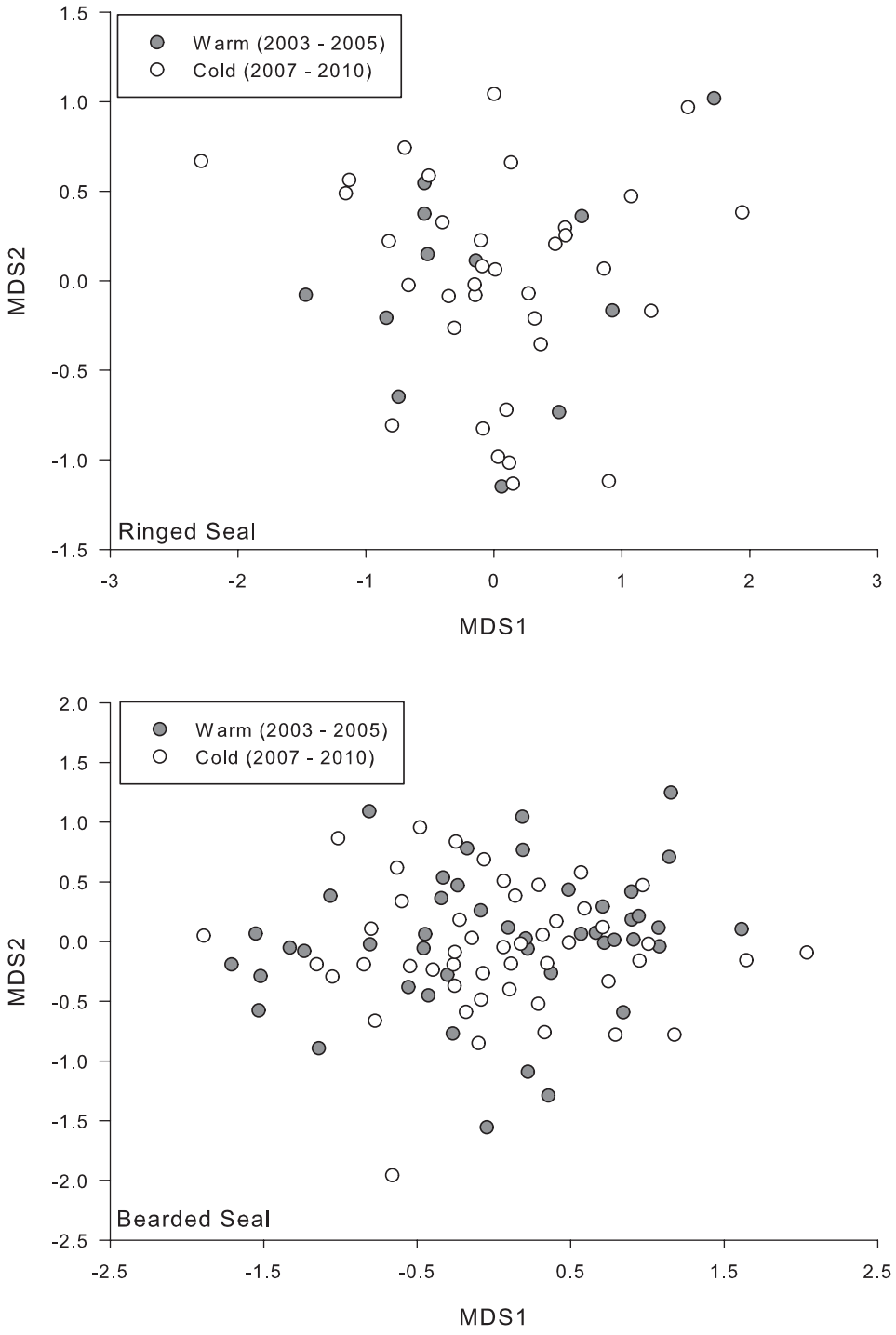


Figure 3.2. nMDS plot of adult ringed and bearded seals using fatty acid (FA) profiles from warm and cold years in the Bering Sea. 2D stress = 0.09 and 0.18, respectively. FA profiles were not different between Bering Sea warm and cold years for ringed (PERMANOVA *P=0.576*) or bearded seals (PERMANOVA *P=0.261*)

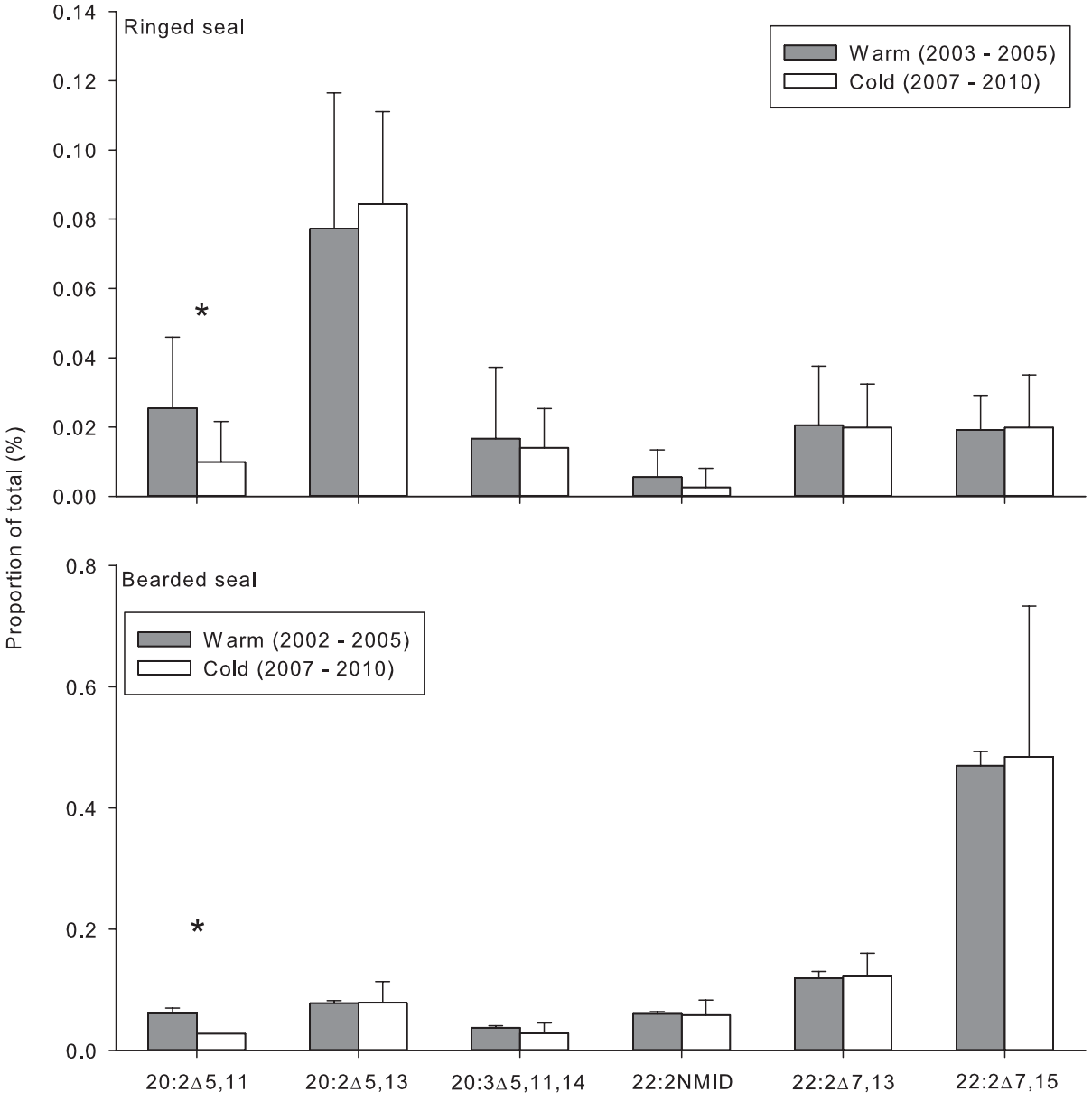


Figure 3.3. Proportions of non-methylene interrupted (NMI) fatty acids (FAs) found in full-thickness blubber of adult ringed and bearded seals during warm and cold years in the Bering Sea (Stabeno et al. 2012a). NMI FA with '*' indicate a significant difference between warm and cold years in the Bering Sea (Mann-Whitney U-test $P<0.013$). Symbols and whiskers represent mean + 1SE

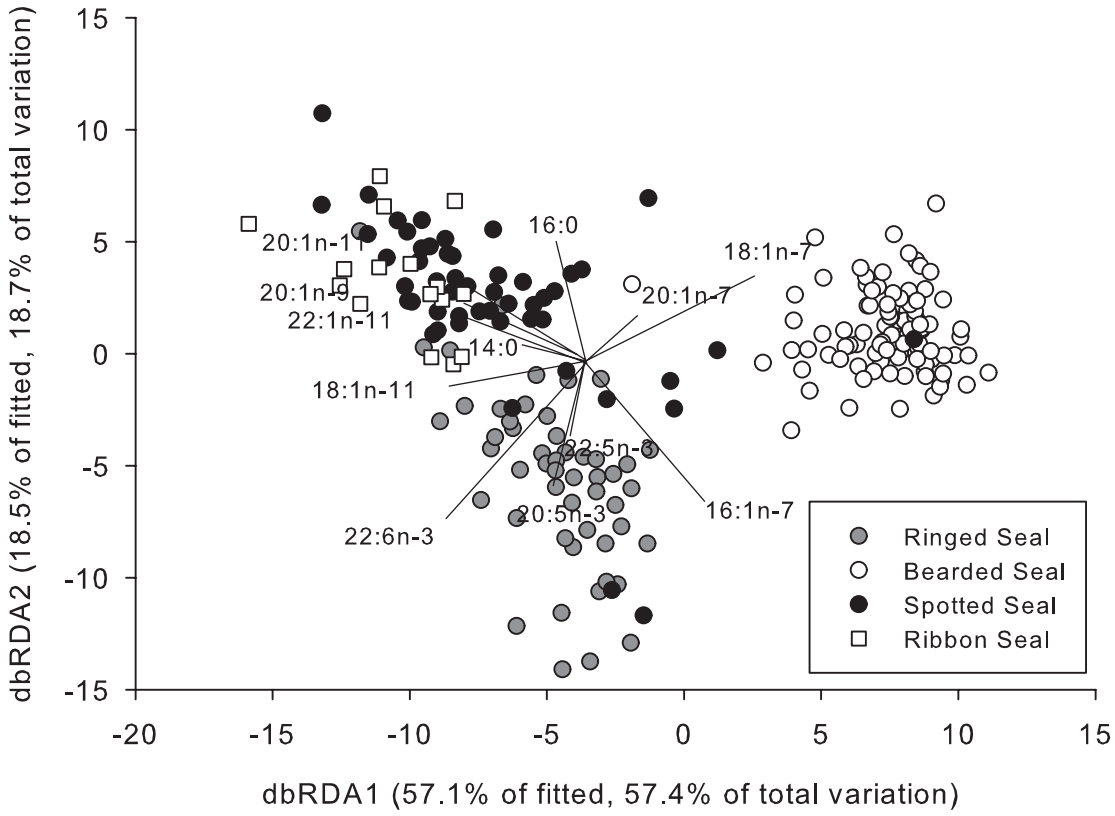


Figure 3.4. Biplot of the distance-based redundancy analysis (dbRDA) relating the variability of fatty acid (FA) composition of adult ringed, bearded, spotted, and ribbon seals. Vectors point toward the direction of maximum change. Key FAs that are significantly correlated with dbRDA axes are shown (multiple correlation >0.2). Sample sizes are given in Table 3.1

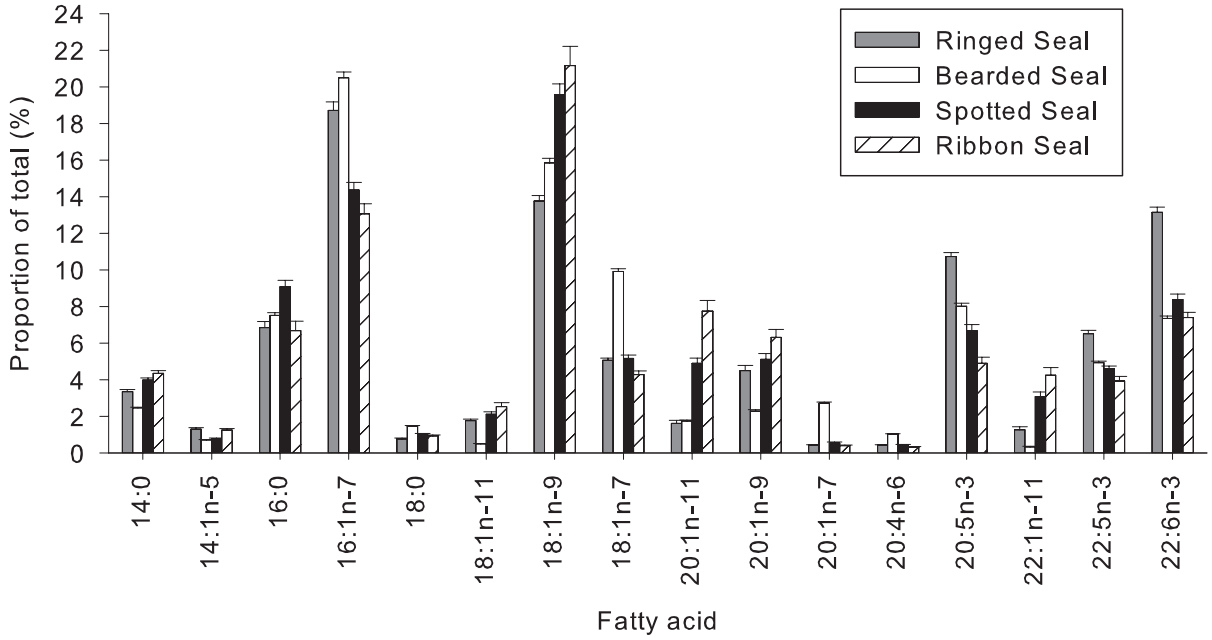


Figure 3.5. Proportions of fatty acids (FAs) > 1% that were primarily responsible for the significant difference (PERMANOVA $P<0.001$) in full-thickness blubber FA composition among adult ringed, bearded, and spotted seals as indicated by SIMPER analysis. FAs for ribbon seals also shown for comparison. Sample sizes are given in Table 3.1. Bars and whiskers represent mean + 1SE, respectively

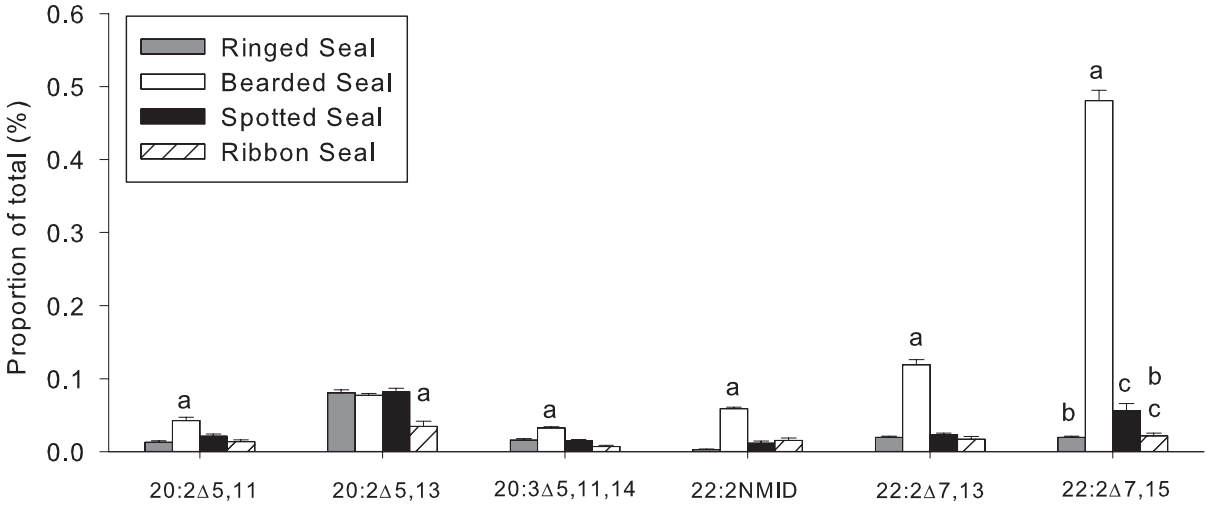


Figure 3.6. Proportions of non-methylene interrupted fatty acids (FAs) in full-thickness blubber of adult ringed, bearded, spotted, and ribbon seals. Groups with different letters are significantly different (Kruskal–Wallis ANOVA $P<0.037$). Sample sizes are given in Table 3.1. Bars and whiskers represent mean + 1SE, respectively

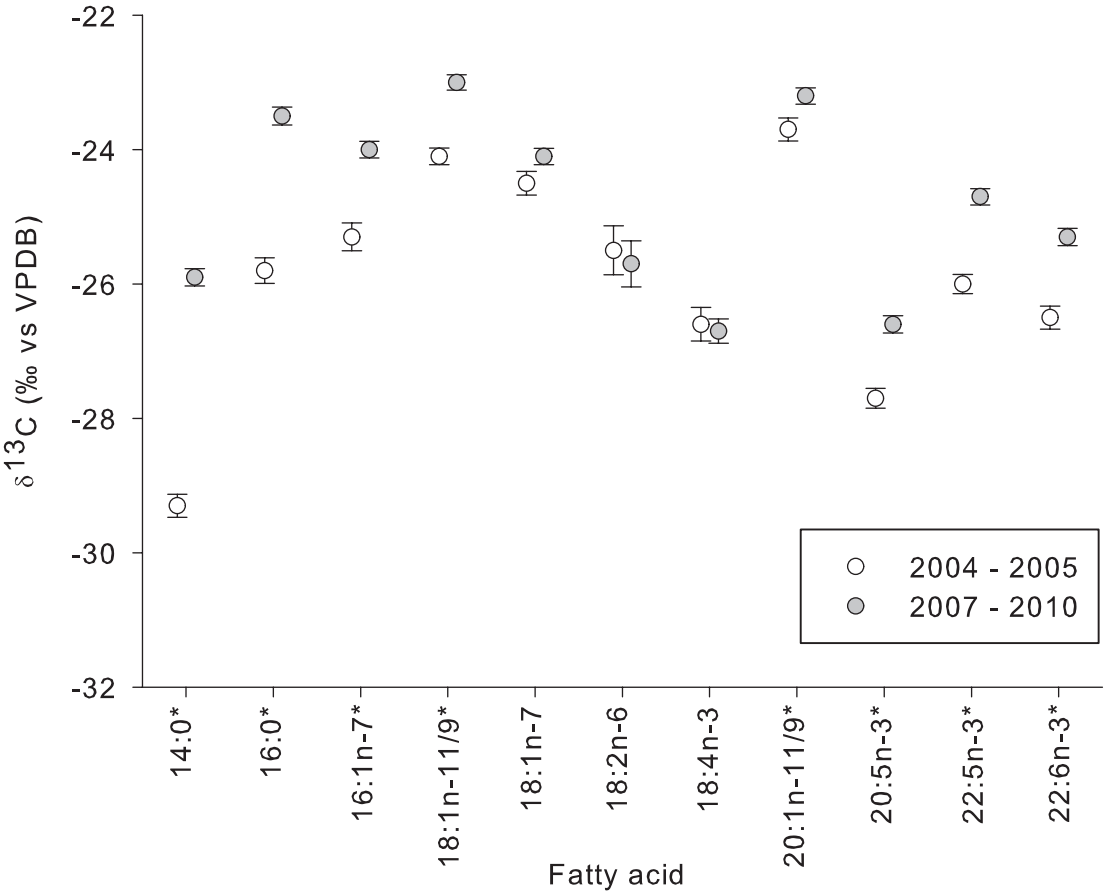


Figure 3.7. $\delta^{13}C$ values for 11 fatty acids (FA) of adult bearded seals in 2004 – 2005 (Bering Sea warm period; *n*=32) and 2007 – 2010 (Bering Sea cold period; *n*=48) (Stabeno et al. 2012a). *indicates FAs with a significant difference between seals collected in 2004 – 2005 and 2007 – 2010 (Mann-Whitney U-test, $P<0.008$). Sample sizes are given in Table 3.1. Symbols and whiskers represent mean ± 1SE, respectively

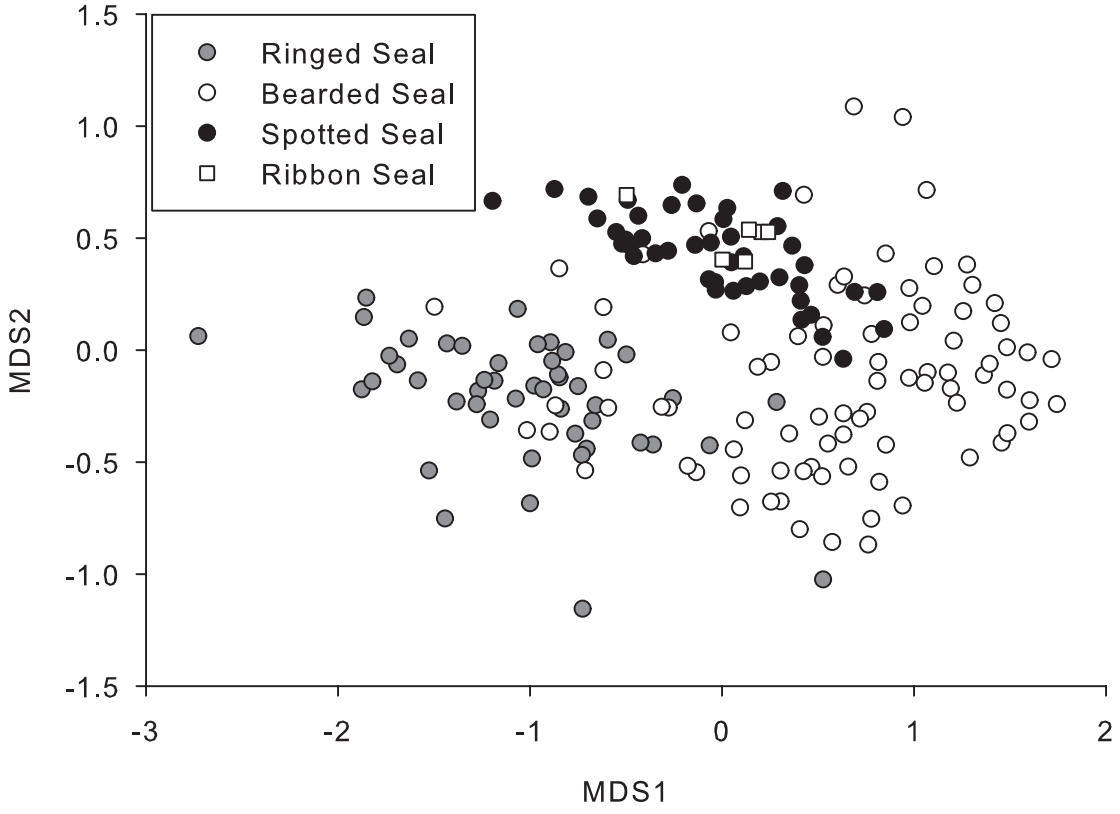


Figure 3.8. Non-metric multidimensional scaling (nMDS) plot of the $\delta^{13}C_{FA}$ values of 11 fatty acids of adult ringed, bearded, spotted, and ribbon seals. 2D stress = 0.07

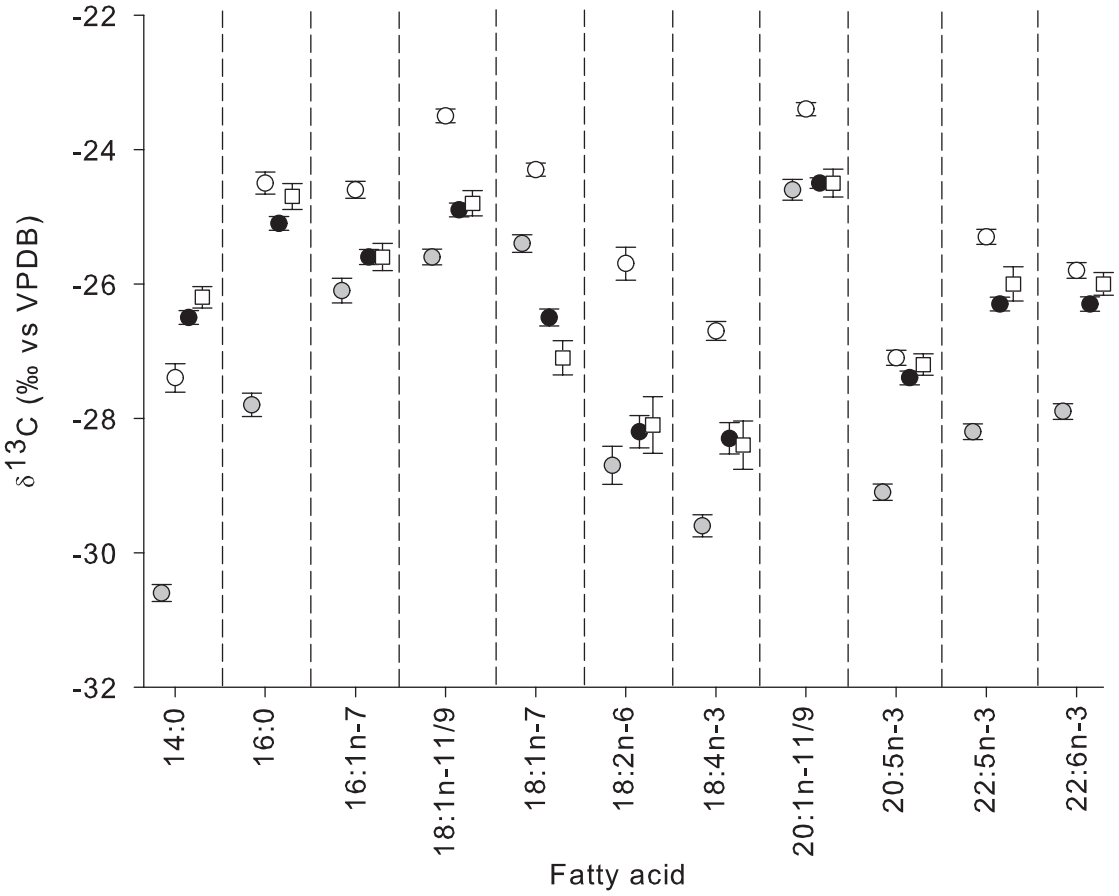


Figure 3.9. $\delta^{13}C$ values for 11 fatty acids of adult ringed, bearded, spotted, and ribbon seals. Ringed=shaded circles, bearded=open circles=, spotted=closed circles, and ribbon seals=open squares. Samples are pooled by species. Sample sizes are given in Table 3.1. Symbols and whiskers represent mean ± 1SE, respectively

Appendix 3.1. Sample sizes for blubber collected from adult ringed, bearded, spotted, and ribbon seals by year, season, and location. SS = Spring-Summer, FW = Fall-Winter. [a]Data from samples from Cooper et al. (2009), [b]Data from samples from Budge et al. (2007).

Ringed Seal

Year	Season	Hooper Bay	Gambell	Savoonga	Nome	Little Diomede	Shishmaref	Kivalina	Point Hope	Total
2002	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2003	SS	0	0	0	0	**1**[a]	0	0	0	**1**
	FW	0	0	0	0	**2**	**3**	0	0	**5**
2004	SS	0	0	0	0	**1**	0	0	0	**1**
	FW	0	0	0	0	0	0	0	0	0
2005	SS	0	0	0	0	**1**	0	0	**1**	**2**
	FW	**1**	0	0	0	**1**	**1**	0	0	**3**
2006	SS	**1**	0	0	0	0	0	0	0	**1**
	FW	**2**	0	0	0	**1**	0	0	0	**3**
2007	SS	**2**	0	0	0	0	0	0	0	**2**
	FW	0	**1**	0	0	0	**2**	0	0	**3**
2008	SS	0	0	0	0	**2**	0	0	0	**2**
	FW	**2**	0	0	0	0	**8**	0	0	**10**
2009	SS	**2**	0	**2**	0	**2**	0	0	**1**	**7**
	FW	**7**	0	0	0	**1**	0	0	0	**8**
2010	SS	0	0	0	0	**2**	0	0	**1**	**3**
	FW	0	0	0	0	0	0	0	0	0

Appendix 3.1. Continued…

Bearded Seal

Year	Season	Hooper Bay	Gambell	Savoonga	Nome	Little Diomede	Shishmaref	Kivalina	Point Hope	Total
2002	SS	0	0	0	0	**7**[b]	0	0	0	**7**
	FW	0	0	0	0	0	0	0	0	0
2003	SS	0	0	0	0	**6**[a]	0	0	0	**6**
	FW	0	0	0	0	0	0	0	0	0
2004	SS	0	0	**1**	**1**	**5**	0	0	0	**7**
	FW	0	0	0	0	**2**	0	0	0	**2**
2005	SS	0	0	0	0	**12**	0	**3**	**10**	**25**
	FW	0	0	0	0	0	0	0	0	0
2006	SS	**1**	0	0	0	0	0	0	**5**	**6**
	FW	0	0	0	0	0	0	0	0	0
2007	SS	0	**2**	0	0	**3**	0	0	**3**	**8**
	FW	0	0	0	0	0	0	0	0	0
2008	SS	0	0	0	0	0	0	0	**11**	**11**
	FW	0	0	0	0	0	0	0	0	0
2009	SS	0	0	**1**	0	**5**	0	0	**4**	**10**
	FW	0	0	0	0	0	0	0	0	0
2010	SS	0	0	0	0	**3**	0	0	**17**	**20**
	FW	0	0	0	0	0	0	0	0	0

Appendix 3.1. Continued…

Spotted Seal

Year	Season	Hooper Bay	Gambell	Savoonga	Nome	Little Diomede	Shishmaref	Kivalina	Point Hope	Total
2002	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2003	SS	0	0	0	0	**9**[a]	0	0	0	**9**
	FW	**1**	0	0	0	0	0	0	0	**1**
2004	SS	0	0	**1**	0	0	0	0	0	**1**
	FW	0	0	0	0	0	**2**	0	0	**2**
2005	SS	0	0	0	0	0	0	0	0	0
	FW	**1**	0	0	0	**2**	0	0	0	**3**
2006	SS	**1**	0	0	0	**1**	0	0	0	**2**
	FW	0	0	0	**1**	0	0	0	0	**1**
2007	SS	0	0	0	0	0	0	0	0	0
	FW	0	**2**	0	0	**1**	**4**	0	0	**7**
2008	SS	0	0	0	0	0	0	0	0	0
	FW	**2**	0	0	**1**	0	**11**	0	0	**14**
2009	SS	0	0	0	0	0	0	0	0	0
	FW	0	**1**	0	0	0	**10**	0	0	**11**
2010	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0

Appendix 3.1. Continued…

Ribbon Seal

Year	Season	Hooper Bay	Gambell	Savoonga	Nome	Little Diomede	Shishmaref	Kivalina	Point Hope	Total
2002	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2003	SS	0	0	0	0	**15**[a]	0	0	0	**15**
	FW	0	0	0	0	0	0	0	0	0
2004	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2005	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2006	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2007	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2008	SS	0	0	0	0	0	0	0	**1**	**1**
	FW	0	0	0	0	0	0	0	0	0
2009	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0
2010	SS	0	0	0	0	0	0	0	0	0
	FW	0	0	0	0	0	0	0	0	0

Appendix 3.2. Proportions of fatty acids (FA) in blubber of adult ringed, bearded, spotted, and ribbon seals used in the data analyses. Data from 2002 are from Budge et al. (2007), and some data from 2003 are from Cooper et al. (2009). Data are presented by species, season, and year. The following FAs were also identified in some samples, but values are not provided because they were < 0.1% of the total across all samples and not included in the data analyses: 12:0, 13:0, i-14:0, 14:1n-7, ai-15:0, 15:1n-8, 15:1n-6, i-16:0, 16:1n-5, 17:1(a), i-17:0, 16:2n-6, 17:1(b), 16:3n-3, 16:4n-3, 18:2Δ5,11, 18:2n-7, 18:3n-1, 20:0, 20:2n-9, 20:2n-6, 20:3n-6, 20:3n-3n, 22:0, 22:1n-7, 22:2n-6, 23:0, 22:4n-3, and 24:1.

Ringed Seal	Spring-Summer 2003 (*n*=1)		Fall-Winter 2003 (*n*=5)		Spring-Summer 2004 (*n*=1)		Spring-Summer 2005 (*n*=2)		Fall-Winter 2005 (*n*=3)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	3.96	na	3.53	1.38	3.13	na	3.33	0.56	3.62	1.27
i-15:0	0.17	na	0.15	0.06	0.15	na	0.10	0.00	0.13	0.02
15:0	0.23	na	0.25	0.09	0.23	na	0.19	0.02	0.23	0.02
16:0	7.06	na	7.88	3.55	6.38	na	6.82	2.00	7.43	2.69
ai-17:0	0.11	na	0.10	0.03	0.09	na	0.07	0.00	0.08	0.01
17:0	0.11	na	0.11	0.05	0.11	na	0.07	0.01	0.10	0.01
18:0	0.90	na	0.87	0.48	0.82	na	0.63	0.20	0.81	0.25
14:1n-9	0.17	na	0.14	0.06	0.15	na	0.08	0.01	0.09	0.03
14:1n-5	1.07	na	1.31	0.69	1.02	na	1.35	0.19	1.14	0.55
16:1n-11	0.56	na	0.30	0.16	0.20	na	0.15	0.02	0.25	0.05
16:1n-9	0.42	na	0.48	0.17	0.44	na	0.36	0.08	0.36	0.08
16:1n-7	14.94	na	18.66	2.14	15.28	na	22.08	3.97	19.03	3.76
17:1(b)	0.13	na	0.22	0.03	0.23	na	0.15	0.04	0.15	0.03
17:1	0.24	na	0.30	0.09	0.24	na	0.22	0.02	0.24	0.08
18:1n-13	0.18	na	0.16	0.08	0.15	na	0.11	0.01	0.15	0.03
18:1n-11	2.48	na	1.79	0.75	3.02	na	1.26	0.08	1.60	0.74
18:1n-9	13.27	na	14.48	1.99	13.33	na	13.75	0.37	13.22	1.89
18:1n-7	4.58	na	4.87	0.62	4.28	na	5.33	0.39	5.10	1.02
18:1n-5	0.59	na	0.61	0.10	0.68	na	0.44	0.06	0.49	0.12
20:1n-11	2.74	na	1.31	0.68	2.15	na	0.99	0.03	1.19	0.60
20:1n-9	6.24	na	5.80	1.36	8.86	na	2.91	0.30	4.40	1.56
20:1n-7	0.44	na	0.45	0.09	0.47	na	0.33	0.03	0.42	0.11
22:1n-11	1.67	na	1.66	0.95	1.60	na	0.25	0.01	0.93	0.52
22:1n-9	0.35	na	0.36	0.14	0.48	na	0.15	0.01	0.29	0.16
16:2n-4	0.66	na	0.46	0.09	0.42	na	0.75	0.10	0.67	0.13
16:3n-4	0.33	na	0.24	0.08	0.24	na	0.26	0.05	0.32	0.02
16:4n-1	0.41	na	0.32	0.08	0.34	na	0.31	0.05	0.42	0.03
18:2n-6	0.72	na	0.74	0.20	0.70	na	0.64	0.03	0.70	0.12
18:2n-4	0.14	na	0.12	0.02	0.13	na	0.10	0.01	0.12	0.03
18:3n-6	0.14	na	0.10	0.02	0.10	na	0.17	0.06	0.12	0.02
18:3n-4	0.10	na	0.11	0.01	0.11	na	0.10	0.00	0.12	0.03
18:3n-3	0.40	na	0.41	0.15	0.37	na	0.39	0.08	0.39	0.09
18:4n-3	1.08	na	0.90	0.04	0.99	na	0.90	0.20	1.02	0.10
18:4n-1	0.16	na	0.11	0.03	0.12	na	0.10	0.00	0.13	0.04
20:4n-6	0.51	na	0.46	0.16	0.44	na	0.38	0.00	0.43	0.03
20:4n-3	0.38	na	0.35	0.06	0.39	na	0.33	0.02	0.34	0.07
20:5n-3	10.68	na	9.21	1.98	8.70	na	12.43	0.99	11.82	0.73
21:5n-3	0.51	na	0.37	0.05	0.41	na	0.53	0.14	0.48	0.04
22:4n-6	0.10	na	0.09	0.05	0.12	na	0.08	0.00	0.09	0.03
22:5n-6	0.12	na	0.13	0.02	0.15	na	0.11	0.02	0.11	0.02
22:5n-3	6.92	na	5.20	1.95	6.77	na	6.94	1.56	6.88	1.30
22:6n-3	12.13	na	12.44	2.65	13.65	na	12.48	3.36	12.50	2.29
20:2Δ5,11	0.01	na	0.04	0.02	0.02	na	0.01	0.01	0.02	0.02
20:2Δ5,13	0.02	na	0.09	0.04	0.08	na	0.09	0.04	0.06	0.03
20:3Δ5,11,14	0.00	na	0.01	0.00	0.02	na	0.04	0.06	0.01	0.00
22:2NMID	0.00	na	0.01	0.01	0.00	na	0.00	0.00	0.00	0.00
22:2Δ7,13	0.00	na	0.03	0.02	0.02	na	0.02	0.00	0.01	0.01
22:2Δ7,15	0.01	na	0.02	0.01	0.02	na	0.03	0.02	0.02	0.01

Appendix 3.2. Continued…

Ringed Seal	Spring-Summer 2006 (*n*=1)		Fall-Winter 2006 (*n*=3)		Spring-Summer 2007 (*n*=2)		Fall-Winter 2007 (*n*=3)		Spring-Summer 2008 (*n*=2)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	2.52	na	2.34	0.82	3.48	0.24	3.94	0.42	3.08	0.35
i-15:0	0.13	na	0.10	0.00	0.12	0.01	0.15	0.01	0.11	0.01
15:0	0.19	na	0.15	0.04	0.25	0.03	0.26	0.02	0.20	0.01
16:0	4.34	na	4.13	2.57	8.49	1.02	8.84	1.73	5.73	1.52
ai-17:0	0.07	na	0.07	0.01	0.10	0.01	0.09	0.01	0.08	0.00
17:0	0.09	na	0.05	0.03	0.13	0.01	0.11	0.01	0.08	0.01
18:0	0.53	na	0.40	0.29	1.04	0.17	0.92	0.11	0.72	0.31
14:1n-9	0.13	na	0.10	0.01	0.10	0.04	0.11	0.02	0.12	0.03
14:1n-5	1.31	na	2.33	0.65	0.84	0.12	0.89	0.18	1.47	0.38
16:1n-11	0.19	na	0.16	0.03	0.19	0.02	0.16	0.03	0.18	0.05
16:1n-9	0.43	na	0.55	0.16	0.32	0.02	0.34	0.05	0.37	0.10
16:1n-7	16.48	na	21.71	2.55	17.88	2.37	18.15	2.28	19.92	0.03
17:1(b)	0.17	na	0.16	0.03	0.17	0.00	0.18	0.03	0.16	0.00
17:1	0.28	na	0.27	0.06	0.28	0.07	0.23	0.03	0.22	0.03
18:1n-13	0.12	na	0.10	0.01	0.17	0.01	0.14	0.03	0.11	0.01
18:1n-11	2.54	na	1.44	0.25	1.22	0.64	1.54	0.56	1.72	0.52
18:1n-9	12.16	na	16.13	0.77	13.80	1.01	12.86	1.44	14.43	0.54
18:1n-7	4.23	na	4.96	1.36	5.84	1.14	5.33	0.49	5.37	0.52
18:1n-5	0.60	na	0.42	0.03	0.61	0.12	0.59	0.11	0.51	0.04
20:1n-11	1.27	na	0.83	0.29	1.37	0.37	1.73	1.00	1.39	0.18
20:1n-9	6.13	na	2.31	0.35	3.15	1.65	4.53	1.21	3.63	0.42
20:1n-7	0.48	na	0.23	0.09	0.44	0.05	0.46	0.13	0.48	0.02
22:1n-11	1.10	na	0.22	0.11	0.86	0.13	1.28	0.40	0.55	0.02
22:1n-9	0.37	na	0.12	0.05	0.28	0.07	0.36	0.12	0.25	0.01
16:2n-4	0.58	na	0.71	0.10	0.53	0.00	0.55	0.07	0.62	0.02
16:3n-4	0.31	na	0.24	0.04	0.24	0.00	0.28	0.01	0.24	0.01
16:4n-1	0.44	na	0.27	0.05	0.29	0.01	0.32	0.01	0.29	0.02
18:2n-6	0.68	na	0.85	0.02	0.76	0.11	0.76	0.08	0.76	0.16
18:2n-4	0.13	na	0.11	0.03	0.16	0.00	0.12	0.01	0.13	0.02
18:3n-6	0.13	na	0.12	0.01	0.12	0.01	0.13	0.01	0.15	0.00
18:3n-4	0.13	na	0.12	0.02	0.12	0.01	0.11	0.02	0.12	0.01
18:3n-3	0.36	na	0.49	0.05	0.38	0.04	0.43	0.01	0.42	0.13
18:4n-3	0.97	na	0.96	0.23	0.91	0.09	1.19	0.05	0.92	0.23
18:4n-1	0.15	na	0.12	0.02	0.12	0.01	0.10	0.02	0.12	0.05
20:4n-6	0.48	na	0.43	0.08	0.59	0.15	0.41	0.05	0.42	0.00
20:4n-3	0.38	na	0.36	0.03	0.33	0.02	0.33	0.02	0.40	0.10
20:5n-3	11.52	na	12.37	1.92	11.70	0.21	10.30	1.53	10.44	1.22
21:5n-3	0.51	na	0.55	0.08	0.45	0.02	0.43	0.06	0.50	0.03
22:4n-6	0.13	na	0.07	0.03	0.14	0.01	0.09	0.01	0.11	0.01
22:5n-6	0.15	na	0.11	0.01	0.15	0.03	0.13	0.02	0.12	0.03
22:5n-3	8.64	na	7.00	1.11	6.41	1.63	5.80	0.39	7.88	0.12
22:6n-3	16.32	na	13.97	2.59	13.45	1.89	13.12	1.07	13.53	0.40
20:2Δ5,11	0.00	na	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00
20:2Δ5,13	0.07	na	0.06	0.01	0.08	0.01	0.10	0.03	0.09	0.03
20:3Δ5,11,14	0.03	na	0.02	0.03	0.02	0.00	0.01	0.00	0.02	0.00
22:2NMID	0.00	na	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22:2Δ7,13	0.02	na	0.01	0.00	0.01	0.01	0.03	0.01	0.01	0.01
22:2Δ7,15	0.02	na	0.02	0.01	0.02	0.01	0.03	0.02	0.01	0.01

Appendix 3.2. Continued…

Ringed Seal	Fall-Winter 2008 (*n*=10)		Spring-Summer 2009 (*n*=7)		Fall-Winter 2009 (*n*=8)		Spring-Summer 2010 (*n*=3)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	3.61	0.69	3.31	0.93	3.52	0.71	2.16	0.53
i-15:0	0.13	0.02	0.12	0.02	0.15	0.02	0.11	0.02
15:0	0.24	0.03	0.21	0.05	0.25	0.04	0.15	0.03
16:0	7.66	1.85	6.78	3.14	6.89	1.53	3.24	0.98
ai-17:0	0.08	0.01	0.08	0.02	0.10	0.03	0.10	0.02
17:0	0.10	0.02	0.09	0.05	0.10	0.03	0.05	0.02
18:0	0.82	0.23	0.85	0.50	0.74	0.16	0.37	0.13
14:1n-9	0.12	0.03	0.12	0.03	0.12	0.03	0.12	0.03
14:1n-5	1.13	0.46	1.24	0.61	1.15	0.37	2.37	0.25
16:1n-11	0.17	0.03	0.19	0.09	0.20	0.08	0.46	0.30
16:1n-9	0.36	0.11	0.37	0.12	0.38	0.08	0.65	0.17
16:1n-7	19.17	3.50	18.44	4.59	16.76	3.29	21.11	2.95
17:1(b)	0.16	0.03	0.16	0.02	0.18	0.04	0.17	0.05
17:1	0.24	0.05	0.23	0.06	0.28	0.06	0.29	0.04
18:1n-13	0.15	0.04	0.13	0.04	0.18	0.06	0.12	0.01
18:1n-11	1.66	0.62	1.66	0.89	2.07	0.50	1.99	0.74
18:1n-9	13.10	2.62	13.83	1.97	12.68	1.68	17.13	1.34
18:1n-7	5.29	0.84	5.21	1.01	4.74	0.76	4.91	0.82
18:1n-5	0.56	0.08	0.51	0.10	0.58	0.09	0.49	0.07
20:1n-11	2.10	2.12	1.63	0.80	1.91	0.89	1.21	0.35
20:1n-9	4.27	1.93	4.14	2.63	5.79	2.08	2.87	0.38
20:1n-7	0.45	0.12	0.51	0.20	0.52	0.11	0.28	0.10
22:1n-11	1.86	2.25	1.19	1.02	1.67	0.96	0.28	0.02
22:1n-9	0.35	0.21	0.33	0.21	0.40	0.14	0.13	0.03
16:2n-4	0.58	0.08	0.66	0.11	0.60	0.10	0.66	0.10
16:3n-4	0.28	0.05	0.29	0.07	0.33	0.07	0.25	0.05
16:4n-1	0.35	0.08	0.32	0.08	0.41	0.11	0.28	0.05
18:2n-6	0.71	0.11	0.79	0.10	0.72	0.09	0.89	0.05
18:2n-4	0.13	0.02	0.13	0.03	0.15	0.02	0.12	0.00
18:3n-6	0.12	0.02	0.13	0.02	0.11	0.01	0.11	0.01
18:3n-4	0.11	0.02	0.12	0.02	0.13	0.02	0.14	0.02
18:3n-3	0.40	0.06	0.46	0.11	0.44	0.07	0.47	0.05
18:4n-3	0.97	0.18	0.95	0.15	1.15	0.23	0.97	0.05
18:4n-1	0.13	0.04	0.12	0.02	0.14	0.03	0.15	0.02
20:4n-6	0.44	0.07	0.44	0.12	0.45	0.12	0.46	0.11
20:4n-3	0.32	0.05	0.36	0.06	0.41	0.07	0.40	0.04
20:5n-3	10.32	1.43	10.66	1.04	10.87	1.95	11.10	0.51
21:5n-3	0.42	0.03	0.49	0.08	0.45	0.03	0.54	0.05
22:4n-6	0.10	0.02	0.10	0.03	0.11	0.04	0.07	0.04
22:5n-6	0.12	0.01	0.13	0.03	0.15	0.04	0.13	0.04
22:5n-3	5.89	0.54	7.35	1.43	6.55	1.33	6.63	0.63
22:6n-3	12.82	2.16	13.26	2.58	13.24	2.38	13.74	2.79
20:2Δ5,11	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
20:2Δ5,13	0.07	0.01	0.08	0.05	0.10	0.02	0.09	0.02
20:3Δ5,11,14	0.01	0.01	0.01	0.01	0.02	0.01	0.03	0.02
22:2NMID	0.00	0.01	0.00	0.01	0.01	0.01	0.00	0.00
22:2Δ7,13	0.02	0.01	0.02	0.02	0.03	0.01	0.02	0.00
22:2Δ7,15	0.02	0.01	0.01	0.01	0.03	0.02	0.02	0.01

Appendix 3.2. Continued…

Bearded Seal	Spring-Summer 2002 (*n*=7)		Spring-Summer 2003 (*n*=6)		Fall-Winter 2004 (*n*=2)		Spring-Summer 2004 (*n*=7)		Spring-Summer 2005 (*n*=25)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	2.88	0.35	2.52	0.31	2.15	0.08	2.36	0.51	2.46	0.45
i-15:0	0.13	0.04	0.12	0.03	0.08	0.01	0.11	0.03	0.10	0.03
15:0	0.39	0.05	0.37	0.04	0.29	0.05	0.35	0.06	0.37	0.06
16:0	8.59	1.24	7.62	1.42	5.89	0.33	7.33	2.14	7.55	1.52
ai-17:0	0.30	0.05	0.33	0.03	0.25	0.09	0.31	0.01	0.29	0.04
17:0	0.29	0.05	0.26	0.04	0.18	0.04	0.28	0.10	0.28	0.07
18:0	1.63	0.46	1.25	0.15	0.94	0.27	1.53	0.69	1.51	0.50
14:1n-9	0.10	0.03	0.08	0.01	0.09	0.01	0.12	0.03	0.12	0.05
14:1n-5	0.59	0.23	0.79	0.12	1.13	0.31	0.68	0.39	0.72	0.27
16:1n-11	0.46	0.05	0.47	0.06	0.28	0.07	0.36	0.05	0.33	0.09
16:1n-9	0.32	0.03	0.33	0.04	0.36	0.02	0.33	0.04	0.32	0.03
16:1n-7	18.78	3.12	21.77	1.29	21.23	0.21	18.83	3.45	20.30	3.62
17:1(b)	0.19	0.03	0.18	0.02	0.19	0.03	0.18	0.03	0.23	0.04
17:1	0.54	0.11	0.65	0.06	0.61	0.07	0.58	0.12	0.60	0.13
18:1n-13	0.43	0.06	0.52	0.11	0.41	0.16	0.49	0.06	0.49	0.10
18:1n-11	0.54	0.15	0.51	0.21	0.65	0.06	0.50	0.10	0.51	0.18
18:1n-9	14.38	2.39	16.05	1.54	19.78	0.98	16.23	3.22	15.81	2.42
18:1n-7	9.38	1.24	10.36	1.15	9.46	2.95	9.96	0.95	9.86	1.75
18:1n-5	0.56	0.07	0.59	0.07	0.57	0.08	0.62	0.11	0.54	0.10
20:1n-11	1.90	0.25	1.76	0.38	1.71	0.36	2.04	0.56	1.81	0.53
20:1n-9	2.48	0.54	2.30	0.32	1.92	0.21	2.38	0.55	2.52	1.29
20:1n-7	2.61	0.58	2.42	0.38	1.88	1.08	3.00	1.07	2.79	0.68
22:1n-11	0.49	0.28	0.31	0.06	0.24	0.05	0.44	0.25	0.39	0.39
22:1n-9	0.17	0.08	0.17	0.09	0.19	0.06	0.28	0.09	0.26	0.09
16:2n-4	0.45	0.05	0.40	0.04	0.39	0.04	0.41	0.05	0.42	0.05
16:3n-4	0.24	0.07	0.20	0.02	0.15	0.02	0.22	0.06	0.22	0.06
16:4n-1	0.38	0.14	0.27	0.06	0.20	0.03	0.32	0.13	0.32	0.10
18:2n-6	0.84	0.07	0.91	0.13	1.00	0.22	0.96	0.19	0.88	0.11
18:2n-4	0.27	0.02	0.26	0.02	0.25	0.08	0.29	0.03	0.26	0.04
18:3n-6	0.13	0.02	0.13	0.01	0.10	0.04	0.13	0.04	0.13	0.02
18:3n-4	0.25	0.03	0.19	0.04	0.28	0.10	0.28	0.05	0.28	0.04
18:3n-3	0.23	0.04	0.21	0.04	0.27	0.05	0.23	0.03	0.26	0.06
18:4n-3	0.68	0.15	0.54	0.16	0.46	0.03	0.54	0.10	0.64	0.22
18:4n-1	0.29	0.06	0.25	0.02	0.27	0.04	0.27	0.08	0.27	0.07
20:4n-6	1.16	0.16	1.20	0.11	1.03	0.01	1.06	0.18	0.98	0.16
20:4n-3	0.45	0.07	0.38	0.05	0.43	0.04	0.42	0.03	0.45	0.10
20:5n-3	9.93	1.42	8.63	1.43	7.38	2.34	8.09	1.98	7.68	1.69
21:5n-3	0.58	0.11	0.49	0.09	0.51	0.01	0.60	0.10	0.56	0.09
22:4n-6	0.28	0.06	0.26	0.03	0.24	0.09	0.33	0.09	0.29	0.06
22:5n-6	0.27	0.06	0.26	0.05	0.27	0.10	0.32	0.07	0.28	0.06
22:5n-3	4.93	0.78	4.22	0.77	4.96	0.35	5.36	1.00	4.99	0.70
22:6n-3	7.34	1.08	6.35	0.79	8.22	2.60	7.27	0.81	7.41	1.89
20:2Δ5,11	0.13	0.02	0.17	0.03	0.02	0.03	0.02	0.03	0.03	0.02
20:2Δ5,13	0.08	0.02	0.10	0.01	0.06	0.01	0.09	0.02	0.07	0.03
20:3Δ5,11,14	0.08	0.02	0.04	0.01	0.02	0.00	0.03	0.01	0.03	0.01
22:2NMID	0.05	0.02	0.06	0.02	0.03	0.02	0.07	0.04	0.06	0.02
22:2Δ7,13	0.12	0.05	0.10	0.04	0.06	0.04	0.17	0.15	0.11	0.06
22:2Δ7,15	0.47	0.05	0.30	0.10	0.52	0.09	0.49	0.19	0.50	0.16

Appendix 3.2. Continued…

Bearded Seal	Spring-Summer 2006 (*n*=6)		Spring-Summer 2007 (*n*=7)		Spring-Summer 2008 (*n*=11)		Spring-Summer 2009 (*n*=10)		Spring-Summer 2010 (*n*=20)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	2.35	0.15	2.49	0.27	2.36	0.34	2.39	0.43	2.52	0.37
i-15:0	0.08	0.02	0.11	0.03	0.09	0.02	0.09	0.02	0.10	0.02
15:0	0.41	0.05	0.36	0.05	0.36	0.03	0.37	0.08	0.38	0.04
16:0	7.00	0.92	7.88	1.16	7.36	1.04	7.32	1.70	7.53	1.02
ai-17:0	0.30	0.05	0.29	0.02	0.30	0.03	0.30	0.04	0.30	0.03
17:0	0.27	0.06	0.29	0.05	0.27	0.05	0.26	0.06	0.29	0.06
18:0	1.22	0.28	1.59	0.29	1.44	0.37	1.38	0.44	1.53	0.34
14:1n-9	0.08	0.01	0.12	0.04	0.09	0.02	0.11	0.10	0.11	0.04
14:1n-5	0.85	0.17	0.59	0.19	0.64	0.12	0.76	0.24	0.71	0.21
16:1n-11	0.33	0.07	0.35	0.05	0.35	0.04	0.34	0.10	0.32	0.06
16:1n-9	0.33	0.02	0.31	0.04	0.31	0.03	0.35	0.04	0.33	0.03
16:1n-7	22.80	1.69	18.89	3.41	20.65	3.02	22.78	4.25	20.15	2.13
17:1(b)	0.26	0.10	0.20	0.04	0.21	0.02	0.21	0.06	0.24	0.08
17:1	0.71	0.08	0.55	0.11	0.60	0.10	0.63	0.16	0.60	0.09
18:1n-13	0.51	0.09	0.51	0.09	0.53	0.07	0.49	0.12	0.51	0.09
18:1n-11	0.53	0.33	0.48	0.14	0.51	0.15	0.55	0.23	0.45	0.14
18:1n-9	16.21	3.13	15.46	2.35	16.21	1.70	16.01	3.34	15.58	2.08
18:1n-7	9.72	1.68	10.50	0.94	10.47	1.13	9.57	1.48	9.82	1.30
18:1n-5	0.47	0.02	0.59	0.09	0.53	0.04	0.52	0.13	0.53	0.07
20:1n-11	1.30	0.26	2.19	0.85	1.70	0.48	1.50	0.32	1.67	0.30
20:1n-9	2.28	1.07	2.24	0.56	2.17	0.26	1.98	0.88	2.14	0.68
20:1n-7	2.20	0.49	3.23	0.76	2.66	0.75	2.20	0.68	2.98	0.62
22:1n-11	0.23	0.12	0.47	0.53	0.24	0.14	0.25	0.19	0.29	0.20
22:1n-9	0.18	0.03	0.31	0.13	0.23	0.06	0.21	0.05	0.24	0.06
16:2n-4	0.40	0.05	0.41	0.02	0.42	0.04	0.42	0.05	0.43	0.07
16:3n-4	0.19	0.03	0.22	0.03	0.21	0.05	0.20	0.05	0.24	0.07
16:4n-1	0.28	0.07	0.33	0.06	0.31	0.08	0.30	0.10	0.37	0.16
18:2n-6	0.94	0.19	0.90	0.11	0.95	0.16	0.92	0.15	0.91	0.11
18:2n-4	0.24	0.05	0.28	0.02	0.27	0.02	0.26	0.02	0.26	0.04
18:3n-6	0.13	0.04	0.14	0.02	0.13	0.01	0.13	0.04	0.13	0.01
18:3n-4	0.28	0.04	0.27	0.03	0.29	0.03	0.28	0.03	0.30	0.04
18:3n-3	0.31	0.07	0.23	0.02	0.25	0.03	0.26	0.05	0.28	0.07
18:4n-3	0.68	0.14	0.57	0.10	0.59	0.16	0.63	0.28	0.69	0.18
18:4n-1	0.26	0.05	0.25	0.05	0.29	0.04	0.27	0.04	0.27	0.07
20:4n-6	1.06	0.34	1.01	0.12	1.04	0.15	1.06	0.20	0.96	0.15
20:4n-3	0.48	0.05	0.38	0.03	0.43	0.06	0.45	0.08	0.47	0.07
20:5n-3	7.68	2.18	8.05	1.76	7.93	1.50	8.16	1.38	7.71	1.68
21:5n-3	0.49	0.11	0.59	0.09	0.57	0.09	0.48	0.04	0.60	0.10
22:4n-6	0.26	0.07	0.32	0.05	0.28	0.07	0.26	0.04	0.28	0.05
22:5n-6	0.23	0.02	0.30	0.05	0.27	0.06	0.24	0.03	0.29	0.06
22:5n-3	4.42	0.64	5.04	0.79	4.81	0.83	4.86	0.44	5.15	0.76
22:6n-3	7.51	1.36	7.03	0.67	7.19	1.12	6.92	2.00	7.88	1.33
20:2Δ5,11	0.02	0.02	0.04	0.02	0.03	0.02	0.03	0.02	0.02	0.02
20:2Δ5,13	0.06	0.02	0.09	0.03	0.07	0.02	0.07	0.02	0.08	0.02
20:3Δ5,11,14	0.03	0.01	0.03	0.00	0.03	0.01	0.03	0.01	0.03	0.01
22:2NMID	0.05	0.02	0.08	0.03	0.06	0.02	0.05	0.01	0.06	0.02
22:2Δ7,13	0.09	0.03	0.20	0.10	0.10	0.04	0.08	0.01	0.13	0.06
22:2Δ7,15	0.54	0.13	0.45	0.09	0.48	0.19	0.55	0.12	0.46	0.09

Appendix 3.2. Continued…

Spotted Seal	Spring-Summer 2003 (*n*=9)		Fall-Winter 2003 (*n*=1)		Spring-Summer 2004 (*n*=1)		Fall-Winter 2004 (*n*=2)		Fall-Winter 2005 (*n*=3)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	4.38	0.64	3.72	na	3.28	na	3.15	0.47	4.23	1.88
i-15:0	0.16	0.02	0.14	na	0.12	na	0.17	0.05	0.14	0.03
15:0	0.24	0.03	0.24	na	0.26	na	0.39	0.12	0.27	0.03
16:0	7.78	1.74	6.88	na	10.67	na	10.09	1.40	8.61	3.83
ai-17:0	0.11	0.02	0.11	na	0.14	na	0.32	0.15	0.10	0.02
17:0	0.09	0.02	0.09	na	0.24	na	0.22	0.02	0.12	0.03
18:0	0.85	0.25	0.78	na	1.81	na	1.24	0.01	0.88	0.20
14:1n-9	0.18	0.03	0.15	na	0.10	na	0.14	0.05	0.12	0.03
14:1n-5	0.90	0.31	1.04	na	0.47	na	0.59	0.15	0.83	0.29
16:1n-11	0.44	0.18	0.16	na	0.32	na	0.35	0.11	0.22	0.05
16:1n-9	0.36	0.08	0.39	na	0.37	na	0.42	0.00	0.34	0.15
16:1n-7	13.10	2.79	14.44	na	9.72	na	15.82	0.84	13.83	1.86
17:1(b)	0.15	0.04	0.18	na	0.31	na	0.34	0.01	0.25	0.08
17:1	0.28	0.05	0.33	na	0.43	na	0.53	0.15	0.38	0.19
18:1n-13	0.25	0.06	0.27	na	0.29	na	0.40	0.04	0.30	0.10
18:1n-11	2.53	0.90	3.94	na	1.93	na	1.08	0.17	2.51	1.34
18:1n-9	21.96	1.91	21.52	na	22.65	na	18.51	0.60	21.86	7.82
18:1n-7	4.44	0.52	4.62	na	4.53	na	5.88	1.26	4.75	0.65
18:1n-5	0.53	0.05	0.53	na	0.50	na	0.47	0.04	0.53	0.08
20:1n-11	6.31	1.20	5.26	na	4.63	na	2.43	0.31	4.64	1.49
20:1n-9	8.41	1.78	8.21	na	3.15	na	4.23	2.08	5.19	1.41
20:1n-7	0.41	0.21	0.00	na	0.43	na	1.74	0.42	0.45	0.10
22:1n-11	3.91	2.07	2.60	na	1.80	na	2.07	2.04	3.04	1.86
22:1n-9	0.49	0.23	0.39	na	0.28	na	0.33	0.12	0.53	0.04
16:2n-4	0.46	0.08	0.46	na	0.27	na	0.33	0.10	0.43	0.23
16:3n-4	0.24	0.06	0.22	na	0.16	na	0.21	0.07	0.22	0.14
16:4n-1	0.31	0.08	0.33	na	0.21	na	0.26	0.11	0.34	0.27
18:2n-6	0.96	0.08	1.02	na	1.15	na	0.93	0.31	1.02	0.18
18:2n-4	0.12	0.02	0.12	na	0.13	na	0.15	0.04	0.14	0.02
18:3n-6	0.08	0.02	0.07	na	0.07	na	0.10	0.03	0.07	0.02
18:3n-4	0.11	0.03	0.15	na	0.15	na	0.15	0.04	0.17	0.03
18:3n-3	0.36	0.05	0.42	na	0.55	na	0.50	0.31	0.47	0.04
18:4n-3	0.77	0.11	0.84	na	0.82	na	0.72	0.04	0.99	0.28
18:4n-1	0.13	0.04	0.15	na	0.09	na	0.13	0.06	0.18	0.04
20:4n-6	0.36	0.07	0.39	na	0.61	na	1.06	0.05	0.41	0.10
20:4n-3	0.29	0.06	0.37	na	0.56	na	0.30	0.02	0.56	0.21
20:5n-3	4.44	1.10	5.31	na	4.12	na	7.18	2.11	6.46	2.49
21:5n-3	0.32	0.07	0.31	na	0.36	na	0.36	0.18	0.35	0.06
22:4n-6	0.08	0.03	0.07	na	0.25	na	0.35	0.03	0.08	0.03
22:5n-6	0.09	0.02	0.11	na	0.21	na	0.26	0.00	0.13	0.05
22:5n-3	3.95	1.04	4.09	na	6.75	na	4.87	1.42	4.17	0.62
22:6n-3	6.65	1.08	7.55	na	12.82	na	8.44	1.37	7.39	1.46
20:2Δ5,11	0.03	0.03	0.05	na	0.02	na	0.04	0.03	0.03	0.01
20:2Δ5,13	0.04	0.03	0.07	na	0.10	na	0.08	0.03	0.09	0.02
20:3Δ5,11,14	0.02	0.01	0.00	na	0.02	na	0.02	0.01	0.01	0.01
22:2NMID	0.02	0.02	0.00	na	0.02	na	0.06	0.06	0.00	0.00
22:2Δ7,13	0.02	0.02	0.01	na	0.02	na	0.04	0.02	0.03	0.00
22:2Δ7,15	0.04	0.02	0.05	na	0.05	na	0.03	0.00	0.05	0.01

Appendix 3.2. Continued…

Spotted Seal	Fall-Winter 2006 (*n*=1)		Spring-Summer 2006 (*n*=2)		Fall-Winter 2007 (*n*=7)		Fall-Winter 2008 (*n*=14)		Fall-Winter 2009 (*n*=11)	
FA	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD	Mean	1SD
14:0	1.99	na	3.77	0.36	4.03	1.07	4.09	0.78	3.87	0.47
i-15:0	0.06	na	0.13	0.00	0.12	0.02	0.14	0.03	0.15	0.04
15:0	0.28	na	0.20	0.01	0.25	0.06	0.26	0.04	0.27	0.04
16:0	6.15	na	6.42	0.43	10.42	3.77	9.48	1.91	9.59	1.69
ai-17:0	0.26	na	0.08	0.00	0.09	0.01	0.11	0.03	0.10	0.02
17:0	0.19	na	0.07	0.02	0.12	0.05	0.12	0.04	0.11	0.03
18:0	1.15	na	0.56	0.05	1.17	0.46	1.12	0.27	1.03	0.21
14:1n-9	0.07	na	0.15	0.01	0.12	0.02	0.12	0.02	0.14	0.02
14:1n-5	0.70	na	1.20	0.12	0.71	0.53	0.73	0.41	0.65	0.23
16:1n-11	0.30	na	0.19	0.01	0.29	0.11	0.24	0.11	0.26	0.12
16:1n-9	0.34	na	0.41	0.03	0.30	0.13	0.29	0.09	0.28	0.07
16:1n-7	22.95	na	14.87	0.48	15.50	3.27	14.88	3.14	13.47	2.08
17:1(b)	0.17	na	0.16	0.01	0.16	0.05	0.18	0.05	0.20	0.03
17:1	0.63	na	0.29	0.01	0.25	0.06	0.28	0.08	0.30	0.05
18:1n-13	0.53	na	0.29	0.03	0.20	0.06	0.25	0.06	0.27	0.07
18:1n-11	0.35	na	4.25	0.13	1.30	0.61	1.83	0.68	2.37	0.68
18:1n-9	20.93	na	23.35	0.50	16.86	1.55	16.46	4.78	21.65	2.02
18:1n-7	12.13	na	4.90	0.15	5.56	0.92	5.23	0.93	4.96	0.73
18:1n-5	0.55	na	0.47	0.02	0.48	0.09	0.55	0.08	0.54	0.07
20:1n-11	1.33	na	7.05	0.49	3.29	2.04	4.72	2.08	5.48	1.64
20:1n-9	1.88	na	6.96	0.27	3.07	1.29	4.07	1.48	5.05	1.44
20:1n-7	2.04	na	0.37	0.01	0.51	0.18	0.52	0.11	0.46	0.18
22:1n-11	0.13	na	2.34	0.25	2.24	1.46	3.15	1.89	3.67	1.60
22:1n-9	0.17	na	0.33	0.01	0.40	0.19	0.42	0.17	0.45	0.13
16:2n-4	0.44	na	0.46	0.01	0.58	0.10	0.56	0.13	0.44	0.07
16:3n-4	0.17	na	0.20	0.01	0.31	0.07	0.32	0.10	0.22	0.04
16:4n-1	0.26	na	0.23	0.01	0.40	0.14	0.44	0.17	0.26	0.07
18:2n-6	1.01	na	0.94	0.03	0.81	0.13	0.85	0.13	0.88	0.13
18:2n-4	0.31	na	0.10	0.01	0.17	0.05	0.17	0.03	0.12	0.02
18:3n-6	0.11	na	0.06	0.00	0.11	0.02	0.10	0.02	0.07	0.01
18:3n-4	0.28	na	0.14	0.01	0.16	0.04	0.15	0.02	0.14	0.02
18:3n-3	0.21	na	0.33	0.01	0.40	0.09	0.41	0.06	0.45	0.10
18:4n-3	0.40	na	0.61	0.00	1.01	0.14	1.04	0.19	0.87	0.17
18:4n-1	0.25	na	0.11	0.01	0.18	0.06	0.20	0.07	0.12	0.03
20:4n-6	0.72	na	0.32	0.01	0.45	0.07	0.46	0.12	0.36	0.13
20:4n-3	0.37	na	0.24	0.01	0.47	0.15	0.44	0.14	0.42	0.15
20:5n-3	6.30	na	4.36	0.09	9.38	1.53	8.35	2.08	5.48	0.74
21:5n-3	0.49	na	0.29	0.02	0.44	0.08	0.42	0.07	0.30	0.05
22:4n-6	0.18	na	0.07	0.01	0.10	0.03	0.11	0.04	0.09	0.06
22:5n-6	0.25	na	0.09	0.01	0.13	0.04	0.13	0.02	0.12	0.02
22:5n-3	4.86	na	4.10	0.71	5.41	1.65	4.96	0.90	4.12	0.93
22:6n-3	5.11	na	6.53	0.58	9.89	3.17	9.47	1.58	8.00	0.96
20:2Δ5,11	0.06	na	0.03	0.01	0.01	0.01	0.02	0.02	0.01	0.01
20:2Δ5,13	0.05	na	0.09	0.00	0.08	0.02	0.09	0.03	0.10	0.03
20:3Δ5,11,14	0.01	na	0.02	0.01	0.01	0.01	0.01	0.01	0.02	0.02
22:2NMID	0.04	na	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
22:2Δ7,13	0.06	na	0.02	0.01	0.02	0.02	0.03	0.01	0.02	0.01
22:2Δ7,15	0.52	na	0.07	0.03	0.07	0.04	0.04	0.02	0.05	0.02

Appendix 3.2. Continued…

Ribbon Seal	Spring-Summer 2003 (*n*=15)		Spring-Summer 2008 (*n*=1)	
FA	Mean	1SD	Mean	1SD
14:0	4.47	0.73	4.23	na
i-15:0	0.17	0.03	0.11	na
15:0	0.23	0.03	0.21	na
16:0	6.55	2.00	8.27	na
ai-17:0	0.10	0.01	0.07	na
17:0	0.09	0.02	0.10	na
18:0	0.91	0.23	1.16	na
14:1n-9	0.16	0.03	0.15	na
14:1n-5	1.24	0.35	0.93	na
16:1n-11	0.40	0.07	0.17	na
16:1n-9	0.29	0.05	0.26	na
16:1n-7	12.67	2.38	15.15	na
17:1(b)	0.21	0.06	0.19	na
17:1	0.29	0.07	0.24	na
18:1n-13	0.20	0.05	0.24	na
18:1n-11	2.57	0.87	3.40	na
18:1n-9	20.65	4.88	19.60	na
18:1n-7	4.13	0.84	5.07	na
18:1n-5	0.54	0.06	0.51	na
20:1n-11	8.11	2.51	6.25	na
20:1n-9	6.67	1.94	4.73	na
20:1n-7	0.39	0.15	0.44	na
22:1n-11	4.61	2.08	3.89	na
22:1n-9	0.60	0.19	0.55	na
16:2n-4	0.49	0.08	0.61	na
16:3n-4	0.26	0.09	0.28	na
16:4n-1	0.37	0.16	0.40	na
18:2n-6	1.05	0.16	0.88	na
18:2n-4	0.12	0.02	0.12	na
18:3n-6	0.09	0.02	0.09	na
18:3n-4	0.12	0.03	0.16	na
18:3n-3	0.45	0.09	0.33	na
18:4n-3	0.93	0.26	0.78	na
18:4n-1	0.18	0.05	0.21	na
20:4n-6	0.32	0.10	0.30	na
20:4n-3	0.53	0.06	0.40	na
20:5n-3	4.78	1.24	6.55	na
21:5n-3	0.42	0.08	0.38	na
22:4n-6	0.06	0.04	0.05	na
22:5n-6	0.10	0.04	0.07	na
22:5n-3	3.93	1.01	3.65	na
22:6n-3	7.48	1.19	7.07	na
20:2Δ5,11	0.01	0.01	0.01	na
20:2Δ5,13	0.03	0.03	0.10	na
20:3Δ5,11,14	0.01	0.01	0.00	na
22:2NMID	0.02	0.01	0.00	na
22:2Δ7,13	0.02	0.01	0.00	na
22:2Δ7,15	0.02	0.02	0.03	na

Appendix 3.3. SIMPER results for annual comparisons with fatty acids (FAs) contributing to differences among years within adult ringed, bearded, and spotted seals. Only years with significant differences among FA profiles are shown (PERMANOVA pairwise comparisons, $P<0.05$; Table 3). Contrib% = % contribution to the mean dissimilarity, Cum% = cumulative contribution. % under years compared = mean dissimilarity between years.

Ringed Seal	2005 vs. 2010 8.86%			2006 vs. 2007 9.74%			2006 vs. 2008 9.44%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%	FA	Contrib%	Cum%
16:0	12.06	12.06	16:0	11.53	11.53	16:0	9.73	9.73
14:1n-5	8.02	20.08	14:1n-5	8.17	19.69	22:1n-11	9.54	19.27
14:0	6.80	26.87	22:1n-11	7.53	27.22	20:1n-9	7.54	26.81
18:1n-11	5.27	32.14	20:1n-9	6.94	34.16	14:1n-5	6.50	33.31
22:1n-11	4.54	36.68	14:0	6.03	40.18	20:1n-11	6.09	39.39
18:0	4.49	41.17	18:0	5.60	45.78	14:0	5.51	44.90
18:1n-9	4.32	45.49	20:1n-11	5.49	51.27	18:0	4.46	49.36
20:1n-9	4.03	49.52	18:1n-11	4.15	55.41	18:1n-11	4.05	53.42
22:6n-3	3.75	53.27	22:5n-3	3.45	58.86	18:1n-7	3.39	56.81
16:1n-9	3.68	56.95	18:1n-7	3.40	62.26	18:1n-9	3.34	60.15
16:1n-11	3.67	60.62	16:1n-7	2.73	64.99	22:5n-3	3.26	63.41
20:1n-11	3.61	64.23	18:1n-9	2.71	67.70	22:6n-3	3.25	66.66
16:1n-7	2.91	67.14	22:6n-3	2.58	70.28	20:5n-3	2.94	69.60
22:5n-3	2.61	69.74	22:1n-9	2.51	72.79	16:1n-7	2.87	72.47
18:1n-7	2.51	72.25	20:1n-7	2.35	75.14	22:1n-9	2.72	75.19
18:2n-6	2.32	74.57	20:5n-3	2.32	77.46	20:1n-7	2.46	77.66
20:1n-7	1.80	76.37	16:1n-9	2.22	79.68	16:1n-9	2.22	79.87
22:1n-9	1.64	78.01	18:4n-3	1.73	81.41	18:4n-3	1.66	81.53
20:5n-3	1.51	79.52	18:1n-5	1.69	83.10	18:1n-5	1.34	82.87
16:4n-1	1.46	80.98	16:2n-4	1.48	84.58	18:2n-6	1.29	84.16
18:3n-3	1.31	82.30	15:0	1.36	85.94	21:5n-3	1.24	85.41
16:2n-4	1.26	83.55	21:5n-3	1.17	87.11	16:2n-4	1.23	86.63
17:1	1.11	84.66	20:4n-6	1.15	88.26	16:4n-1	1.20	87.83
18:1n-5	1.08	85.74	17:0	0.93	89.19	18:3n-3	1.13	88.96
15:0	1.04	86.78	16:4n-1	0.90	90.09	16:0	1.05	90.01
20:4n-6	1.01	87.79						
21:5n-3	1.00	88.79						
18:4n-3	1.00	89.79						
20:4n-3	0.98	90.77						

Appendix 3.3. Continued…

Ringed Seal	2006 vs. 2009 10.05%			2007 vs. 2010 10.54%			2008 vs. 2010 9.83%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%	FA	Contrib%	Cum%
22:1n-11	9.23	9.23	16:0	13.01	13.01	16:0	11.12	11.12
16:0	8.71	17.93	14:1n-5	9.19	22.20	22:1n-11	9.31	20.44
20:1n-9	8.43	26.37	22:1n-11	7.64	29.84	14:1n-5	7.54	27.98
20:1n-11	6.23	32.60	14:0	6.46	36.30	14:0	6.03	34.00
14:1n-5	6.14	38.74	18:0	5.76	42.06	20:1n-9	5.43	39.43
14:0	5.23	43.97	20:1n-9	4.97	47.03	18:0	4.57	44.01
18:0	4.23	48.20	18:1n-11	4.49	51.52	20:1n-11	4.41	48.41
18:1n-11	4.23	52.42	20:1n-11	4.01	55.53	18:1n-9	4.23	52.65
16:1n-7	3.74	56.17	18:1n-9	3.76	59.29	18:1n-11	4.22	56.86
22:6n-3	3.13	59.30	16:1n-9	3.32	62.61	16:1n-11	3.52	60.38
18:1n-7	3.00	62.30	16:1n-11	3.27	65.87	16:1n-9	3.27	63.65
22:1n-9	2.90	65.20	16:1n-7	2.54	68.41	22:6n-3	2.98	66.63
18:1n-9	2.90	68.10	22:1n-9	2.53	70.94	22:1n-9	2.63	69.26
20:1n-7	2.89	70.99	22:6n-3	2.38	73.32	16:1n-7	2.45	71.71
22:5n-3	2.85	73.84	18:1n-7	2.23	75.54	18:1n-7	2.33	74.05
20:5n-3	2.57	76.42	20:1n-7	2.09	77.63	20:1n-7	2.22	76.26
16:1n-9	1.92	78.34	22:5n-3	2.04	79.67	22:5n-3	1.98	78.24
18:4n-3	1.81	80.15	15:0	1.43	81.10	20:5n-3	1.73	79.97
18:1n-5	1.38	81.53	20:5n-3	1.40	82.50	18:2n-6	1.67	81.64
16:4n-1	1.33	82.86	18:1n-5	1.27	83.77	15:0	1.19	82.83
20:4n-6	1.15	84.01	16:2n-4	1.27	85.03	18:4n-3	1.18	84.01
16:2n-4	1.14	85.15	18:4n-3	1.24	86.27	21:5n-3	1.18	85.19
15:0	1.05	86.20	20:4n-6	1.23	87.50	16:2n-4	1.13	86.32
18:3n-3	1.02	87.22	18:2n-6	1.09	88.59	20:4n-3	1.06	87.38
18:2n-6	1.01	88.23	21:5n-3	1.06	89.66	18:3n-3	1.05	88.43
21:5n-3	0.98	89.21	17:0	1.02	90.68	20:4n-6	1.04	89.46
16:3n-4	0.91	90.13				16:4n-1	1.02	90.49

Appendix 3.3. Continued…

Ringed Seal	2009 vs. 2010 10.54%	
FA	Contrib%	Cum%
16:0	9.61	9.61
22:1n-11	9.25	18.86
14:1n-5	6.97	25.83
20:1n-9	6.97	32.79
14:0	5.60	38.40
20:1n-11	4.94	43.33
18:0	4.20	47.53
18:1n-11	4.10	51.63
18:1n-9	3.88	55.51
16:1n-7	3.71	59.22
16:1n-11	3.22	62.43
22:6n-3	2.99	65.42
22:1n-9	2.97	68.39
16:1n-9	2.87	71.26
20:1n-7	2.73	73.99
18:1n-7	2.32	76.31
22:5n-3	2.11	78.42
20:5n-3	1.69	80.11
18:4n-3	1.41	81.52
18:2n-6	1.25	82.77
20:4n-6	1.25	84.03
16:4n-1	1.24	85.26
15:0	1.14	86.4
18:1n-5	1.09	87.49
16:2n-4	1.03	88.52
21:5n-3	0.91	89.43
16:3n-4	0.88	90.31

Appendix 3.3 Continued…

Bearded Seal	2002 vs. 2006 7.62%			2002 vs. 2009 7.63%			2002 vs. 2010 6.72%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%	FA	Contrib%	Cum%
20:5n-3	5.91	5.91	20:1n-9	5.82	5.82	20:5n-3	6.27	6.27
20:1n-9	5.82	11.73	20:1n-7	4.72	10.54	20:1n-9	5.05	11.32
20:1n-11	4.68	16.41	22:6n-3	4.69	15.23	22:1n-11	4.72	16.04
16:1n-7	4.28	20.69	16:1n-7	4.67	19.91	20:1n-7	4.22	20.26
22:1n-11	4.14	24.83	18:1n-9	4.52	24.42	22:6n-3	3.82	24.08
20:1n-7	4.13	28.95	22:1n-11	4.47	28.90	18:1n-9	3.81	27.89
18:0	4.06	33.01	20:5n-3	4.47	33.36	18:0	3.70	31.58
16:0	3.95	36.96	16:0	4.39	37.75	16:0	3.69	35.27
14:1n-5	3.74	40.71	18:0	4.18	41.94	14:1n-5	3.61	38.89
18:1n-9	3.72	44.43	20:1n-11	3.51	45.44	16:1n-7	3.46	42.35
18:1n-11	3.51	47.94	14:1n-5	3.38	48.83	22:5n-3	3.30	45.65
22:6n-3	3.21	51.15	14:0	3.33	52.16	14:0	3.13	48.78
22:5n-3	3.14	54.29	18:1n-11	2.98	55.14	18:1n-7	3.04	51.82
14:0	3.04	57.33	18:4n-3	2.90	58.04	20:1n-11	2.84	54.66
20:4n-6	2.91	60.24	18:1n-7	2.88	60.92	18:1n-11	2.82	57.47
18:1n-7	2.85	63.09	22:5n-3	2.35	63.27	20:4n-6	2.66	60.13
17:1	2.42	65.51	16:4n-1	2.13	65.40	20:2Δ5,11	2.42	62.55
20:2Δ5,11	2.11	67.61	17:1	2.12	67.52	16:4n-1	2.42	64.97
16:4n-1	2.00	69.61	20:4n-6	2.04	69.55	18:4n-3	2.41	67.38
18:4n-3	1.90	71.51	20:2Δ5,11	1.94	71.50	16:1n-11	2.32	69.70
21:5n-3	1.87	73.38	16:1n-11	1.86	73.35	22:1n-9	2.00	71.70
16:1n-11	1.86	75.23	21:5n-3	1.75	75.10	17:1	1.85	73.56
18:2n-6	1.60	76.83	22:2Δ7,15	1.62	76.72	21:5n-3	1.70	75.25
18:1n-13	1.45	78.28	18:1n-13	1.61	78.34	18:1n-13	1.67	76.92
22:2Δ7,15	1.40	79.68	18:1n-5	1.61	79.95	16:3n-4	1.32	78.24
18:3n-3	1.40	81.08	22:1n-9	1.49	81.44	18:4n-1	1.30	79.54
17:1(b)	1.30	82.38	18:2n-6	1.29	82.72	22:2Δ7,15	1.27	80.81
18:1n-5	1.23	83.61	15:0	1.14	83.86	18:2n-6	1.23	82.04
22:1n-9	1.22	84.83	16:3n-4	1.12	84.98	17:1(b)	1.18	83.23
22:4n-6	1.20	86.02	17:0	1.08	86.07	20:4n-3	1.18	84.41
16:3n-4	1.05	87.07	20:4n-3	1.06	87.13	22:5n-6	1.18	85.59
17:0	1.03	88.10	20:3Δ5,11,14	1.03	88.16	22:2Δ7,13	1.17	86.76
20:3Δ5,11,14	1.03	89.13	14:1n-9	0.98	89.14	18:1n-5	1.17	87.93
18:4n-1	0.99	90.12	22:2Δ7,13	0.97	90.11	18:3n-3	1.16	89.09
						20:3Δ5,11,14	1.13	90.22

Appendix 3.3 Continued…

Bearded Seal	2003 vs. 2010 6.61%			2006 vs. 2007 7.59%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%
22:6n-3	5.10	5.10	20:1n-11	7.06	7.06
22:5n-3	4.81	9.91	20:1n-7	6.06	13.12
20:5n-3	4.78	14.69	20:1n-9	5.99	19.12
20:1n-9	4.45	19.15	20:5n-3	5.01	24.13
20:1n-7	4.32	23.47	22:1n-11	4.46	28.58
16:0	3.69	27.16	16:1n-7	4.24	32.83
20:1n-11	3.30	30.46	18:0	3.53	36.35
18:0	3.28	33.75	18:1n-9	3.49	39.84
18:4n-3	3.24	36.99	14:1n-5	3.47	43.31
20:2Δ5,11	3.23	40.21	18:1n-11	3.42	46.73
22:2Δ7,15	3.02	43.24	16:0	3.20	49.93
20:4n-6	2.96	46.20	22:5n-3	3.18	53.11
18:1n-7	2.95	49.15	18:1n-7	3.08	56.19
18:1n-11	2.94	52.09	22:6n-3	3.01	59.20
22:1n-11	2.88	54.97	20:4n-6	2.94	62.13
18:1n-9	2.86	57.83	22:1n-9	2.33	64.47
14:1n-5	2.76	60.60	17:1	2.25	66.72
16:1n-11	2.63	63.23	22:2Δ7,13	2.05	68.77
16:1n-7	2.57	65.79	18:4n-3	2.02	70.78
14:0	2.26	68.05	21:5n-3	1.85	72.63
16:4n-1	2.24	70.29	22:2Δ7,15	1.75	74.39
21:5n-3	2.13	72.42	18:1n-5	1.74	76.13
18:3n-4	2.13	74.54	18:2n-6	1.66	77.78
22:1n-9	2.08	76.62	20:4n-3	1.43	79.22
20:4n-3	1.64	78.25	18:3n-3	1.35	80.56
18:1n-13	1.63	79.88	14:00	1.34	81.9
18:2n-6	1.58	81.46	16:4n-1	1.33	83.23
18:3n-3	1.41	82.88	22:4n-6	1.29	84.52
17:1(b)	1.32	84.20	17:1(b)	1.25	85.77
18:1n-5	1.27	85.47	18:1n-13	1.23	87.01
17:1	1.26	86.73	22:5n-6	1.19	88.20
16:3n-4	1.21	87.94	15:0	1.03	89.23
22:5n-6	1.13	89.08	17:0	1.02	90.25
16:2n-4	1.12	90.20			

Appendix 3.3 Continued…

Spotted Seal	2004 vs. 2007 11.76%			2004 vs. 2008 11.16%			2004 vs. 2009 10.59%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%	FA	Contrib%	Cum%
22:1n-11	7.02	7.02	22:1n-11	8.4	8.40	22:1n-11	8.99	8.99
20:1n-11	5.80	12.81	20:1n-11	6.16	14.56	20:1n-11	7.11	16.10
20:1n-7	5.71	18.52	20:1n-7	5.76	20.32	20:1n-7	6.46	22.57
20:5n-3	5.37	23.89	20:5n-3	4.9	25.22	18:1n-11	5.37	27.94
20:1n-9	4.30	28.19	20:1n-9	4.36	29.58	20:4n-6	4.98	32.91
16:0	4.05	32.24	18:1n-9	3.85	33.43	20:1n-9	4.94	37.85
22:6n-3	3.62	35.86	20:4n-6	3.76	37.19	22:5n-3	4.23	42.09
20:4n-6	3.58	39.44	18:1n-11	3.75	40.94	20:5n-3	3.62	45.70
14:0	3.47	42.91	16:1n-7	3.32	44.26	22:6n-3	3.30	49.00
18:1n-11	3.42	46.33	22:5n-3	3.03	47.29	16:1n-7	3.28	52.28
22:5n-3	3.31	49.64	14:0	2.92	50.21	22:4n-6	2.82	55.10
16:1n-7	3.23	52.87	22:6n-3	2.79	53.00	18:0	2.77	57.87
18:0	2.76	55.63	22:4n-6	2.43	55.43	14:0	2.41	60.28
16:2n-4	2.49	58.12	16:2n-4	2.42	57.84	18:1n-7	2.24	62.52
22:4n-6	2.45	60.57	14:1n-5	2.31	60.16	16:0	2.15	64.68
14:1n-5	2.42	62.99	18:0	2.3	62.46	17:1	2.13	66.81
17:1	2.38	65.37	18:1n-7	2.27	64.73	ai-17:0	1.91	68.72
18:1n-9	2.17	67.54	16:0	2.27	67.00	22:1n-9	1.90	70.62
18:1n-7	2.02	69.55	17:1	2.26	69.25	18:3n-3	1.86	72.48
ai-17:0	1.88	71.43	18:4n-3	2.19	71.44	18:2n-6	1.83	74.31
18:2n-6	1.86	73.29	16:4n-1	2.06	73.51	18:1n-9	1.79	76.10
17:1(b)	1.80	75.10	18:2n-6	1.82	75.33	14:1n-5	1.71	77.81
18:3n-3	1.78	76.88	18:3n-3	1.81	77.14	22:5n-6	1.56	79.37
18:4n-3	1.77	78.65	22:1n-9	1.78	78.92	20:4n-3	1.56	80.93
18:1n-13	1.74	80.38	ai-17:0	1.77	80.69	17:0	1.53	82.46
22:1n-9	1.67	82.05	17:1(b)	1.62	82.31	16:1n-9	1.49	83.95
16:4n-1	1.63	83.68	16:1n-11	1.52	83.82	16:1n-11	1.49	85.44
16:1n-9	1.54	85.23	16:1n-9	1.44	85.26	17:1(b)	1.47	86.91
20:4n-3	1.51	86.74	16:3n-4	1.43	86.69	16:2n-4	1.39	88.31
22:5n-6	1.32	88.06	20:4n-3	1.43	88.12	18:4n-3	1.27	89.57
17:0	1.29	89.35	22:5n-6	1.36	89.48	21:5n-3	1.16	90.73
16:3n-4	1.26	90.61	17:0	1.3	90.78			

Appendix 3.3 Continued…

Spotted Seal	2007 vs. 2009 10.53%			2008 vs. 2009 8.69%	
FA	Contrib%	Cum%	FA	Contrib%	Cum%
22:1n-11	8.93	8.93	22:1n-11	9.55	9.55
20:1n-11	8.70	17.63	20:1n-11	6.99	16.54
20:5n-3	7.02	24.65	20:5n-3	6.41	22.95
20:1n-9	6.85	31.50	18:1n-9	5.84	28.79
18:1n-11	6.27	37.78	20:1n-9	5.83	34.62
16:0	5.13	42.90	18:1n-11	5.18	39.80
22:5n-3	4.42	47.32	22:5n-3	3.92	43.72
22:6n-3	3.94	51.26	16:0	3.51	47.22
18:1n-9	3.56	54.82	14:1n-5	3.29	50.51
14:1n-5	3.12	57.93	22:6n-3	3.22	53.73
18:0	3.06	60.99	16:1n-7	3.18	56.91
16:1n-7	2.85	63.83	18:1n-7	2.71	59.62
14:0	2.83	66.66	14:0	2.66	62.28
18:1n-7	2.22	68.89	16:4n-1	2.50	64.78
22:1n-9	1.98	70.86	18:0	2.43	67.21
20:1n-7	1.93	72.80	18:4n-3	2.32	69.53
16:4n-1	1.73	74.53	22:1n-9	2.13	71.67
20:4n-3	1.63	76.16	20:1n-7	1.91	73.58
18:4n-3	1.63	77.79	20:4n-6	1.89	75.47
21:5n-3	1.59	79.38	20:4n-3	1.81	77.28
16:2n-4	1.55	80.93	16:2n-4	1.76	79.04
20:4n-6	1.51	82.44	21:5n-3	1.68	80.72
16:1n-11	1.47	83.91	16:1n-11	1.68	82.39
16:1n-9	1.19	85.10	16:3n-4	1.43	83.83
18:3n-3	1.15	86.24	18:2n-6	1.37	85.20
18:2n-6	1.14	87.38	18:4n-1	1.30	86.50
18:1n-13	1.13	88.51	18:3n-3	1.24	87.74
16:3n-4	1.06	89.57	16:1n-9	1.10	88.85
18:1n-5	1.02	90.59	18:1n-13	1.03	89.88
			17:1	1.01	90.89

GENERAL CONCLUSIONS

My dissertation used state-of-the-art analytical techniques to track sympagic and pelagic sources of FAs to consumers in the Bering Sea. There are several advantages to using the $\delta^{13}C_{FA}$ values over FA or bulk stable isotope analyses alone. For instance, it is not possible to estimate the proportional contribution of different sources of primary production using algal marker FAs alone, because they are found in both algae within sea ice and the water column (e.g., Søreide et al. 2008). The relative importance of various sources of primary productivity can be elucidated because these sources have sufficiently different bulk isotopic signatures (Søreide et al. 2006). However, isotopic routing remains an issue with their interpretation because stable isotopes can be incorporated differently into various tissues and compounds such as muscle and adipose tissue (Gannes et al. 1997). By focusing on one tissue type (i.e., fat), and a compound that primarily comes from storage lipids (i.e., FAs), using $\delta^{13}C_{FA}$ values avoids the issue of stable isotope routing. Compound-specific stable isotope analysis is continuing to gain attention and use for studying food webs, and my results provide a foundation for future work in not only the Bering Sea, but also other Arctic marine ecosystems.

Chapter 1 described and compared the FA and $\delta^{13}C_{FA}$ values of sea ice and pelagic organic matter (i-POM and p-POM, respectively) in the Bering Sea. Using FA biomarkers, I found differences in the relative compositions of diatoms, dinoflagellates, and bacteria of i-POM and p-POM. Many i-POM $\delta^{13}C_{FA}$ values were higher (up to ~10 ‰) than those of p-POM. The characteristics of FAs in i-POM and differences from p-POM determined in Chapter 1 subsequently were used to make estimates of the proportional contribution of sympagic FAs to higher trophic levels in the Bering Sea. Chapter 2 examined and compared the foraging strategies of zooplankton (*T. libellula, C. marshallae/glacialis, and T. raschii*), and used the information from Chapter 1 to estimate the proportional contribution of carbon from sea ice organic matter relative to pelagic organic matter to these zooplankton consumers. FA biomarkers confirmed that the amphipod *Themisto libellula* was predominately carnivorous, and the copepod *Calanus marshallae/glacialis* and euphausiid *Thysanoessa raschii* were primarily herbivorous, but displayed some degree of omnivory. Estimates from several stable isotope mixing models using combinations of $\delta^{13}C_{FA}$ values of several FA markers showed that in some cases substantial proportions of FAs in all consumers originated from sea ice-derived organic matter in 2009 and 2010: *T. libellula* 36–72%, *C. marshallae/glacialis* 27–63%, and *T. raschii* 39–71%. Similarly, Chapter 3 compared the FA signatures (as diet indicator) of ringed

(*Pusa/Phoca hispida*), bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ribbon seals (*Histriophoca fasciata*), and used the information from Chapter 1 to estimate the proportional contribution of FAs from sympagic relative to pelagic FAs to ice seal species. FA composition of ice seal blubber showed clear evidence of resource partitioning among them, and little niche separation between spotted and ribbon seals, which is consistent with previous studies (Lowry & Frost 1981, Cooper et al. 2009). Bearded seal FA profiles were reflective of their more benthic feeding compared with the other seal species, while ringed, spotted, and ribbon seal FAs pointed toward a more pelagic diet. The FA composition of primarily pelagic feeding adult ringed seals and predominantly benthic feeding adult bearded seals did not differ between the warm (2002 – 2005) and cold (2007 – 2010) periods in the Bering Sea, suggesting that their diets and possibly food web structure were not affected by these large multiyear environmental fluctuations. However, $\delta^{13}C_{FA}$ values of bearded seals were higher during the cold period than those from the warm period in the Bering Sea, which suggests that although their diets may not have changed between the two periods, the sources of primary production of their prey may have switched from more pelagic to more sympagic origins. Estimates from stable isotope mixing models, using combinations of $\delta^{13}C_{FA}$ values of several FA markers, showed that varying amounts of these FAs in seals originated from sea ice-derived organic matter in 2009 and 2010. Estimates were highest for bearded (62–79%) and spotted seals (51–62%), and lowest for ringed seals (21–60%). These results indicate that sympagic production currently is an important contributor to food webs supporting both benthic and pelagic upper trophic level species in years with heavy ice cover in the Bering Sea, assuming that these seals were mainly foraging in the Bering Sea.

Depending on the timing of pelagic and sympagic production, and the timing of zooplankton reproduction, the zooplankton species I investigated may be more resilient to changes in primary production than sympagic faunal species. Ice endemic species, such as harpacticoid copepods and the amphipods *Gammarus wilkitzkii* and *Apherusa glacialis,* spend their entire life cycles within or under sea ice relying on sea ice as habitat and as a source of food (reviewed in Bluhm et al. 2010). While zooplankton species do not completely rely on sympagic primary production, my results showed that ice algae might play an important role as a food source for zooplankton when phytoplankton production is not available during critical periods in their life history (e.g., Durbin & Casas 2014). Depending on the timing, the increase in net primary productivity in the Arctic Ocean, Chirkov Basin, and a predicted increase in the Bering Sea (Brown & Arrigo 2012) may help offset the expected reduction in ice algal production.

Changes in the food web structure at the lower trophic levels will likely affect upper trophic level consumers, such as fishes, seabirds, and marine mammals. Thus, climate-induced changes to the amount of sea ice algal material that is transferred through the Arctic and sub-Arctic marine food web will likely affect the foraging ecology of ice seals. For example, the weakening of pelagic-benthic coupling due to changes in the timing and strength of primary production could lead to more pelagic foraging strategies in the future. Indeed, bearded seals are generalist feeders and have been shown to feed more pelagically in recent years (Carroll et al. 2013), and spotted seals also display variability and flexibility in their diets (reviewed in Boveng et al. 2009). Consequently, resource partitioning could decrease among ice seals, which would increase competition for prey and may affect their populations.

Though we now have a better understanding of the FA and $\delta^{13}C_{FA}$ characteristics of sea ice and pelagic organic material in the Bering Sea, and also to what degree zooplankton and ice seals use a sea ice-based food web in 2009 and 2010, there is still more research to be done. My suggestions for future work include describing the FA and $\delta^{13}C_{FA}$ characteristics of i-POM and p-POM in years with different environmental conditions (mostly sea ice conditions) for comparison to gain a better understanding if and how these characteristics can be affected by changes in the environment. More importantly, samples should be analyzed from different areas of the Arctic such as the Chukchi and Beaufort seas, especially since these areas have been experiencing opposing trends in seasonal sea ice extent and duration. Controlled feeding experiments of zooplankton and pinnipeds would be valuable to further examine FAs and isotopic turnover rates of FAs, as well as the effect of dietary modification on $\delta^{13}C_{FA}$ values and potential isotopic fractionation of FAs in these consumers.

There are several avenues for potential new research using FAs and compound-specific stable isotope analysis. One is to take a more in depth look at the sources of non-methylene interrupted (NMI) FAs. It is well known that these unusual NMI FAs are present in benthic invertebrates (e.g., Paradis & Ackman 1977, Joseph 1979, 1982, Cook et al. 2000, Pond et al. 2002, Howell et al. 2003, Castell et al. 2004, Kawashima 2005, Zhukova 2007, Monroig et al. 2012) and can be used as biomarkers to identify prey of benthic origin, but not necessarily to species (Budge et al. 2007, Cooper et al. 2009). Thus, efforts to determine if these NMI FA markers can be identified to specific benthic prey species would make a substantial contribution to the use of FA markers in benthic feeders,

such as bearded seals and Pacific walruses (*Odobenus rosmarus divergens*), and the potential competition over resources between them.

In summary, my research provides the first quantitative assessment of the relative importance of sympagic organic matter from the Bering Sea to consumers in the Bering Sea and Arctic. These data also provide an important foundation from which long-term diet monitoring of important zooplankton and ice seal populations can continue. The results presented here are representative of heavy ice conditions in the Bering Sea as they occurred in 2009 and 2010, and may be used as a baseline for comparison with future studies conducted during warmer years with less sea ice cover. The southeastern Bering Sea is one of the most productive ecosystems in the world and supports some of the world's most valuable fisheries (Loughlin & Ohtani 1999). For almost 40 years, changes in climate influencing the extent and timing of sea ice cover have changed the abundance and/or distribution of these resources (reviewed in Aydin & Mueter 2007). A poleward shift in the distribution of temperature-dependent ground fish has been documented in the Bering Sea in recent years (Mueter & Litzow 2008). Thus, changes in the fish communities in the Bering Sea will likely affect the operation of commercial fisheries and also have management implications (Mueter et al. 2011). In addition to ecosystem understanding, tracking the complex interdependencies among arctic marine primary production and arctic marine food webs is of high relevance to Alaskan Native communities using subsistence practices. In general, fluctuations and changes in the Bering Sea have a strong human dimension as the productive Bering Sea shelf supports large stocks of organisms that are harvested commercially and as part of the subsistence lifestyle. Ice seals are of immense cultural and nutritional importance to coastal communities in Alaska and other circumpolar countries. Significant changes, or even the loss, of the ice-based food web and the associated food sources could negatively affect ice seals and the communities that depend on these resources. In addition to my above suggestions for future research, I also strongly recommend collecting POM, zooplankton, and ice seal blubber samples, in addition to samples of other species that were not included in this study, such as fishes (in particular ice-associated fishes), cetaceans, and seabirds for archival and long-term monitoring of diets. Through studying the production sources, diets, and foraging strategies of marine animals over time, we can track their response to climate-induced changes in the marine ecosystem and make better predictions of how they might respond to future changes in their environment.

References

Antonelis G, Melin S, Bukhtiyarov Y (1994) Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74-79

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bahr F, Bates NR, Benitez-Nelson C, Bowler B, Brownlee E, Ehn JK, Frey KE, Garley R, Laney SR, Lubelczyk L, Mathis J, Matsuoka A, Mitchell BG, Moore GWK, Ortega-Retuerta E, Pal S, Polashenski CM, Reynolds RA, Schieber B, Sosik HM, Stephens M, Swift JH (2012) Massive phytoplankton blooms under Arctic sea ice. Science 336:1408

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bates NR, Benitez-Nelson CR, Brownlee E, Frey KE, Laney SR, Mathis J, Matsuoka A, Greg Mitchell B, Moore GWK, Reynolds RA, Sosik HM, Swift JH (2014) Phytoplankton blooms beneath the sea ice in the Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 105:1-16

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biology 25:374-383

Aydim K, Mueter F (2007) The Bering Sea – A dynamic food web perspective. Deep-Sea Research II: Topcial Studies in Oceanography 54:2501-2525

Baier CT, Napp JM (2003) Climate-induced variability in *Calanus marshallae* populations. Journal of Plankton Research 25:771-782

Bluhm BA, Gradinger RR, Schnack-Schiel SB (2010) Sea ice meio- and macrofauna. In: Thomas DN, Dieckmann GS (eds) Sea Ice. Wiley-Blackwell, Oxford, United Kingdom

Boveng PL, Bengtson JL, Buckley TW, Cameron MF, Dahle SP, Kelly BP, Megrey BA, Overland JE, Williamson NJ (2009) Status review of the spotted seal (*Phoca largha*). Book National Oceanic and Atmospheric Admistration Technical Memorandum. NMFS-AFSC-200. U. S. Department of Commerce

Brown ZA, Arrigo KW (2012) Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES Journal of Marine Science: Journal du Conseil 69:1180-1193

Brown ZW, van Dijken GL, Arrigo KR (2011) A reassessment of primary production and environmental change in the Bering Sea. Journal of Geophysical Research 116:1-26

Budge SM, Springer AM, Iverson SJ, Sheffield G (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. Marine Ecology Progress Series 336:305-309

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117-129

Bukhtiyarov Y, Frost KJ, Lowry LF (1984) New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring. In: Fay FH, Fedoseev GA (eds) Soviet-American Cooperative Research on Marine Mammals Volume 1 - Pinnipeds Under Project V6 Marine Mammals, of the US-USSR Agreement on Cooperation in the Field of Enviromental Protection. U. S. Department of Commerce, NOAA Techincal Report NMFS 12, Washington, D. C.

Burns JJ (1971) Biology of the ribbon seal, *Histriophoca fasciata*, in the Bering Sea (Abstract). Proceedings of the Twenty-second Alaska Science Conference. Alaska Division of the American Association for the Advancement of Science, College, AK

Burns JJ (2002) Harbor seal and spotted seal, *Phoca vitulina* and *P. largha*. In: Perrin WF, Würsig B, Thewissen HGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, CA

Burns JJ, Shapiro LH, Fay FH (1981) Ice as marine mammal habitat in the Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle

Carroll SS, Horstmann-Dehn L, Norcross BL (2013) Diet history of ice seals using stable isotope ratios in claw growth bands. Canadian Journal of Zoology:191-202

Castell JD, Kennedy EJ, Robinson SMC, Parsons GJ, Blair TJ, Gonzalez-Duran E (2004) Effect of dietary lipids on fatty acid composition and metabolism in juvenile green sea urchins (*Strongylocentrotus droebachiensis*). Aquaculture 242:417-435

Ciannelli L, Brodeur RD, Napp JM (2004) Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea. Marine Biology 144:515-526

Conover RJ, Huntley M (1991) Copepods in ice-covered seas—Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. Journal of Marine Systems 2:1-41

Cook EJ, Bell MV, Black KD, Kelly MS (2000) Fatty acid compositions of gonadal material and diets of the sea urchin, *Psammechinus miliaris*: trophic and nutritional implications. Journal of Experimental Marine Biology and Ecology 255:261-274

Cooper MH, Budge SM, Springer AM, Sheffield G (2009) Resource partitioning by sympatric pagophilic seals in Alaska: monitoring effects of climate variation with fatty acids. Polar Biology 32:1137-1145

Dehn L-A, Sheffield G, Follmann E, Duffy L, Thomas D, O'Hara T (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biology 30:167-181

Durbin EG, Casas MC (2014) Early reproduction by *Calanus glacialis* in the Northern Bering Sea: the role of ice algae as revealed by molecular analysis. Journal of Plankton Research 36:523-541

Falk-Petersen S, Gatten RR, Sargent JR, Hopkins CCE (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: seasonal changes in the lipid class composition of *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa raschii* (M. Sars), and *T. inermis* (Krøyer). Journal of Experimental Marine Biology and Ecology 54:209-224

Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Canadian Journal of Fisheries and Aquatic Sciences 57:178-191

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web; Proceedings of the 24th European Marine Biology Symposium. In: Barnes M, Gibson RN (eds) Trophic Relationships in the Marine Environment. Aberdeen University Press, Aberdeen

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic Calanus. Marine Biology Research 5:18-39

Fay FH (1974) The role of ice in the ecology of marine mammals in the Bering Sea. In: Hood DW, Kelley EJ (eds) Oceanography of the Bering Sea. Institute of Marine Science, University of Alaska, Fairbanks

Finley KJ, Evans CR (1983) Summer diet of the bearded seal (*Erignathus barbatus*) in the Canadian High Arctic. Arctic 36:82-89

Frost KJ, Lowry LF (1980) Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Canadian Journal of Zoology 58:1601-1607

Frost KJ, Lowry LF (1981) Foods and trophic relationships of cetaceans in the Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle

Gannes, LZ, O'Brien DM, Martínez del Rio D (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78:1271-1276.

Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic Calanus species based on feeding experiments with a ^{13}C labelled diatom. Journal of Experimental Marine Biology and Ecology 317:109-125

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biology 18:53-61

Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313-326

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Research Part II-Topical Studies in Oceanography 49:5131-5150

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Progress In Oceanography 71:182-231

Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Marine Ecology Progress Series 255:193-206

Iverson SJ, Arnould JPY, Boyd IL (1997) Milk fatty acid signatures indicate both major and minor shifts in the diet of lactating Antarctic fur seals. Canadian Journal of Zoology 75:188-197

Joseph JD (1979) Lipid composition of marine and estuarine invertebrates: Porifera and cnidaria. Progress in Lipid Research 18:1-30

Joseph JD (1982) Lipid composition of marine and estuarine invertebrates. Part II: Mollusca. Progress in Lipid Research 21:109-153

Kawashima H (2005) Unusual minor nonmethylene-interrupted di-, tri-, and tetraenoic fatty acids in limpet gonads. Lipids 40:627-630

Kelly BP (1988) Ribbon seal, *Phoca fasciata*. In: Lentfer JW (ed) Selected Marine Mammal Species of Alaska: Species Accounts with Research and Management Recommendations. Marine Mammal Commission, Washington, D.C.

Kürten B, Frutos I, Struck U, Painting SJ, Polunin NVC, Middelburg JJ (2013) Trophodynamics and functional feeding groups of North Sea fauna: a combined stable isotope and fatty acid approach. Biogeochemistry 113:189-212

Loughlin TR, Ohtani K (1999) Dynamics of the Bering Sea, Vol AK-SG-99-03. University of Alaska Sea Grant, Fairbanks, Alaska

Lowry LF (1985) The ribbon seal (*Phoca fasciata*). In: Burns JJ, Frost KJ, Lowry LF (eds) Marine Mammal Species Accounts. Alaska Department of Fish and Game, Juneau, AK

Lowry LF, Frost KJ (1981) Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. In: Hood DW, Calder JA (eds) The Bering Sea Shelf: Oceanography and Resources, Book Office of Marine Pollution Assessment, NOAA. University of Washington Press, Seattle

Lowry LF, Frost KJ, Burns JJ (1980a) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330-342

Lowry LF, Frost KJ, Burns JJ (1980b) Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Canadian Journal of Fisheries and Aquatic Sciences 37:2254-2261

Marion A, Harvey M, Chabot D, Brethes J (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. Marine Ecology Progress Series 373:53-70

Mauchline J, Fischer LR (1969) The Biology of Euphausiids, Vol 7. Academic Press, London and New York

McLaren IA (1958) The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctc. Bulletin Fisheries Research Board Canada 118:1-97

McRoy CP, Goering JJ (1976) Annual budget of primary production in the Bering Sea. Marine Science Communications 2:255-267

Michel C, Legendre L, Ingram RG, Gosselin M, Levasseur M (1996) Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers. Journal of Geophysical Research: Oceans 101:18345-18360

Monroig Ó, Navarro J, Dick J, Alemany F, Tocher D (2012) Identification of a Δ5-like fatty acyl desaturase from the cephalopod *Octopus vulgaris* (Cuvier 1797) involved in the biosynthesis of essential fatty acids. Marine Biotechnology 14:411-422

Mueter FJ, Litzow MA (2008) Sea ice retreat alters biogeography of the Bering Sea continental shelf. Ecological Applications 18:309-320

Mueter FJ, Siddon EC, Hunt Jr. GL (2011) Climate change brings uncertain future for subarctic marine ecosystems and fisheries. In: North by 2020. University of Alaska Press

NMFS (2012a) Endangered and threatened species; threatened status for Beringia and Okhost Distinct Population Segments of the *Erignathus barbatus nauticus* subspecies of the bearded seal; Final Rule. 77:76740-76768

NMFS (2012b) Endangered and threatened species; threatened ttatus for the Arctic, Okhotsk, and Baltic Subspecies of the ringed real and endangered status for the *Ladoga* subspecies of the ringed seal; Final Rule. 77:76706-76738

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biology 32:1559-1570

Paradis M, Ackman R (1977) Potential for employing the distribution of anomalous non-methylene-interrupted dienoic fatty acids in several marine invertebrates as part of food web studies. Lipids 12:170-176

Pinchuk AI, Coyle KO, Farley EV, Renner HM (2013) Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiidae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web. ICES Journal of Marine Science: Journal du Conseil 70:1244-1254

Pond DW, Allen CE, Bell MV, Dover CLV, Fallick AE, Dixon DR, Sargent JR (2002) Origins of long-chain polyunsaturated fatty acids in the hydrothermal vent worms *Ridgea piscesae* and *Protis hydrothermica*. Marine Ecology Progress Series 225:219-226

Quakenbush L, Citta J, Crawford J (2009) Biology of the Spotted Seal (*Phoca largha*) in Alaska from 1962 to 2008. Preliminary Report to National Marine Fisheries Service. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK

Quakenbush L, Citta J, Crawford J (2011) Biology of the Ringed Seal (*Phoca hispida*) in Alaska from 1960-2010. Final Report to National Marine Fisheries Service. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK

Sargent JR, Falk-Petersen S (1981) Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: Lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid-winter. Marine Biology 62:131-137

Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. Hydrobiologia 167-168:101-114

Sato M, Sasaki H, Fukuchi M (2002) Stable isotopic compositions of overwintering copepods in the arctic and subarctic waters and implications to the feeding history. Journal of Marine Systems 38:165-174

Scott CL, Falk-Petersen S, Gulliksen B, Lonne OJ, Sargent JR (2001) Lipid indicators of the diet of the sympagic amphipod *Gammarus wilkitzkii* in the Marginal Ice Zone and in open waters of Svalbard (Arctic). Polar Biology 24:572-576

Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biology 21:65-70

Simpkins MA, Hiruki-Raring LM, Sheffield G, Grebmeier JM, Bengtson JL (2003) Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. Polar Biology 26:577-586

Smith SL (1990) Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. Marine Biology 106:59-69

Smith SL (1991) Growth, development and distribution of the euphausiids *Thysanoessa raschii* (M. Sars) and *Thysanoessa inermis* (Kroyer) in the southeastern Bering Sea. Polar Res 10:461-478

Søreide JE, Carroll ML, Hop H, Ambrose WG, Hegseth EN, Falk-Petersen S (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Marine Biology Research 9:831-850

Søreide JE, Falk-Petersen S, Hegseth EN, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep Sea Research Part II: Topical Studies In Oceanography 55:2225-2244

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Progress In Oceanography 71:59-87

Søreide JE, Leu EVA, Berge J, Graeve M, Falk-Petersen S (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global Change Biology 16:3154-3163

Springer AM, Roseneau DG (1985) Copepod-based food webs: Auklets and oceanography in the Bering Sea. Marine Ecology Progress Series 21:229-237

Stabeno P, Napp J, Mordy C, Whitledge T (2010) Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: Sea ice, tides and winds. Progress In Oceanography 85:180-196

Stevens CJ, Deibel D, Parrish CC (2004) Copepod omnivory in the North Water Polynya (Baffin Bay) during autumn: spatial patterns in lipid composition. Deep-Sea Research Part I-Oceanographic Research Papers 51:1637-1658

Strasburger WW, Hillgruber N, Pinchuk AI, Mueter FJ (2013) Feeding ecology of age-0 walleye pollock (*Gadus chalcogramma*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography. doi:10.1016/j.dsr2.2013.10.007

Thiemann GW, Budge SM, Iverson SJ, Stirling I (2007a) Unusual fatty acid biomarkers reveal age- and sex-specific foraging in polar bears (*Ursus maritimus*). Canadian Journal of Zoology 85:505-517

Thiemann GW, Iverson SJ, Stirling I (2007b) Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. Marine Mammal Science 23:241-261

Thiemann GW, Iverson SJ, Stirling I (2008) Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic. Marine Mammal Science 24:91-111

Tourangeau S, Runge JA (1991) Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. Marine Biology 108:227-233

Walsh JJ, McRoy CP (1986) Ecosystem analysis in the southeastern Bering Sea. Continental Shelf Research 5:259-288

Zhukova N (2007) Lipid classes and fatty acid composition of the tropical nudibranch mollusks *Chromodoris* sp. and *Phyllidia coelestis*. Lipids 42:1169-1175

Ziel HL, Cameron MF, Boveng PL (2008) Spring diet of ribbon and spotted seals in the Bering Sea (Poster presentation). In: Alaska Fisheries Science Center NMFS, NOAA (ed), Seattle, WA

Appendix 1: Operating parameters for FAME analysis with GC-FID (taken from Appendix 7 in Budge et al. 2006 Supplementary Material).

GC column: polar capillary column, 30 m × 0.25 mm ID flexible fused silica column coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness, DB-23, Agilent Technologies, U.S.A.).

Split Injection

A syringe is used to deliver 1 μl of a sample with a concentration of 50 mg/mL to an injector held at a constant temperature of 250°C. The helium split flow is set at a rate of 100 mL/min to generate a split ratio of approximately 1:100. The carrier gas flow rate (He) is 1 mL/min and the flow rates of air and hydrogen to the detector are 450 mL/min and 45 mL/min, respectively. The detector is held at 250°C and the oven temperature program begins at 153°C. It is held at that temperature for 2 min and then ramps at a rate of 2.3°C/min to 174°C. That temperature is maintained for 0.2 min and then ramped at 2.5°C to 210°C. This final temperature is held for 2 min or until just after 24:1 elutes. This program should produce a runtime of approximately 32 min.

Splitless Injection

Injection volume remains the same but a reduced sample concentration of 0.5 mg/mL is used. The temperatures of the injector and detector remain the same. Flow rates of gases to the column and detector are also unchanged. The split flow rate is set at 30 mL/min and the temperature program is modified as follows: the initial temperature is set at 50°C and held for 1 min. The temperature is then rapidly ramped at 45°C/min to 153°C. The program described above is then followed. This results in an approximate 3 min increase in the runtime.